PROGRESS IN THE
PHYSIOLOGY OF FARM ANIMALS

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OF
FARM ANIMALS

Edited by

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School of Agriculture, Cambridge

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PREFACE

During the last twenty years or so much research work has been done on the physiology of farm animals with a view to increasing their efficiency as producers of animal products. As the literature on this is scattered widely in many different journals and known only to specialists, it was thought that a useful purpose would be served if this newer knowledge could be brought together in a book so as to make it available to advanced students and those who are engaged in teaching animal production. Just as the sciences of chemistry and botany have formed the basis of advancement in soils and crop husbandry respectively, so the science of physiology should form the basis of animal husbandry in the future.

As a background for increasing our output of animal products present-day medical and veterinary textbooks cover too narrow a field. By going back to the earlier works such as those of Luciani on human, Colin on comparative, and Meade-Smith on veterinary physiology one obtains a much wider outlook and one much more applicable to problems of animal production.

While the objects of medical and veterinary physiology are the study of the normal workings of the animal body to enable one to detect abnormalities and the effects of disease, farm animal physiology has as its objective the obtaining of control over the functions of the animal body in order to increase efficiency in the output of eggs, offspring, milk, meat and wool, and to maintain good health throughout a long life-time of high production. It is therefore supplementary to medical and veterinary physiology, although it interlocks with the latter on questions of sterility and nutritional disorders.

In the selection of subjects for chapters in this book preference has been given to those in which advance has been rapid in recent years and we have been fortunate in obtaining the co-operation of those who have taken an active part in this progress to write these chapters.

We are grateful to Messrs. Butterworth & Co. for undertaking the publication of this new venture and for all the trouble they have taken in its production. Acknowledgment is also made to all those authors, individually named in the text, who have so kindly allowed their original illustrations to be reproduced here.

JOHN HAMMOND.

School of Agriculture,
Cambridge.
April, 1954.

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NUTRITION AND METABOLISM

CHAPTER 1

RUMINANT NUTRITION

BY K. L. BLAXTER

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THE STUDY of ruminant nutrition in many respects is the study of a remarkable symbiosis between the animal and the vast population of bacteria and infusoria which inhabit its digestive tract. This salient feature of ruminant metabolism makes it well-nigh impossible to apply results of nutritional investigations made with the common laboratory animals to ruminants. Thus with ruminants dietary carbohydrates and protein are subject to much bacterial action in the rumen and to a lesser extent the caecum, before assimilation by the body and subsequent dissimilation in the tissues. This entails an entirely different appraisal of the overall nutritive value of these entities as ration ingredients in ruminants. Again, microbiological activity similarly results in a rapid synthesis of many of the vitamins of the B complex such that it may be virtually impossible to demonstrate a dietary need of the adult host animal for a particular member. Even the mineral elements are involved in this close relationship between the micro-organisms and their host. The ingestion of sodium or potassium oxalate, which in rat and man leads to diminished retention of calcium through formation of insoluble calcium oxalate in the gut, in ruminants leads to disturbances of acid–base equilibrium of an entirely different nature. Other examples may be cited, notably the large dietary requirement of cobalt by the ruminant, its easy assimilation of the phosphorus of plant phytates, and its large dietary requirements for water relative to its size. All are contingent upon the fact that the microbiological population of the rumen occupy such an important role in the animal's economy. As in so many other types of symbiosis, much adaptation of each partner takes place for mutual good. Considered singly some of these adaptations are not necessarily always advantageous.

SOME DEVELOPMENTAL CONSIDERATIONS

During foetal life the fore-stomachs of the calf develop quite early from a long spindle-shaped dilatation of the primitive gut. From this single dilatation, the rumen, reticulum, omasum and abomasum all develop concurrently. Contrary to the views of many of the earlier comparative anatomists, there is thus little basis for the belief that the rumen, reticulum and omasum develop as terminal dilatations of the oesophagus, in fact on anatomical grounds the rumen of the ruminant is homologous to the fundus of the human stomach. The form of the four compartments is clearly visible in cattle embryos measuring but 30 mm. from crown to rump (LAMBERT, 1948). Even at birth, however, these organs have not attained the relative proportions they possess in the adult animal, as shown in *Figure 1.1*. At birth the capacity of the

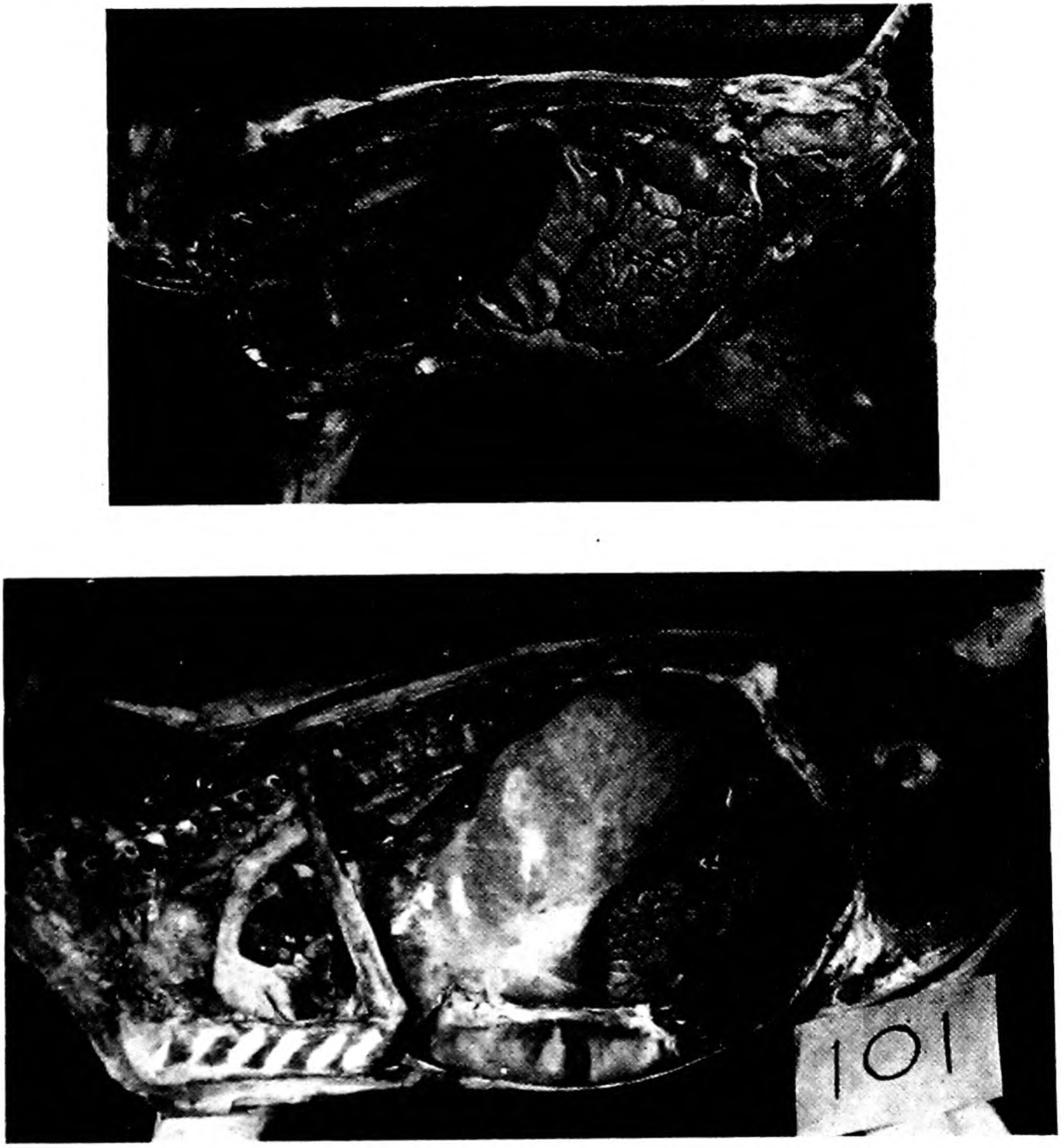


Figure 1.1. The normal development of the fore-stomachs of the young calf during the first three months of life. The upper photograph is of a dissection of a calf at birth, and the lower of a dissection of a calf reared until three months of age on milk, hay and concentrated food. The difference in relative size of the rumen is quite apparent, and it will be seen that as this organ grows it displaces the left kidney toward the midline and also displaces the small intestine. In the adult cow, the rumen occupies a far greater proportion of the abdominal cavity, the relative over-development of the rumen continuing until an age of approximately nine months, when maximal relative size is attained.

abomasum or true stomach is greater than that of the rumen and those organs which in adult life are to contain the vast fermenting food mass show many signs of underdevelopment. The papillae of the rumen wall are soft and short, the spaces between the leaves of the omasum are not fully patent, and the honeycomb-like structure of the wall of the reticulum is particularly deficient.

During the period when the young ruminant subsists on milk, considerable growth of the rumen takes place, but the most important impetus to its development appears to be the ingestion of solid food. Artificial prolongation of the period during which milk is fed retards the growth of the fore-stomachs, but does not stop it. Even surgical removal of a major part of the rumen is followed by its complete regeneration at this stage. Although experiments have shown that early dependence on roughage will accelerate rumen development, it nevertheless takes nearly a year before adult relative proportions of the four compartments are attained (BLAXTER *et al* 1952).

One feature of the ruminant stomachs of particular importance in early life is the so-called oesophageal groove. Contraction of the lips of this groove makes a tube-like structure which effectively by-passes the rumen and reticulum and allows liquid food to pass from the oesophagus direct to the abomasum where true gastric digestion takes place. The stimulus to the formation of this by-pass is the presence of fluid in the back of the mouth and can be elicited by stimulation of the glossopharyngeal nerve. It appears to be a simple reflex act in which the efferent nerve supply has been traced to fibres in the vagus nerve. The reflex is maximal in the very young lamb or calf and becomes less easily elicited as the animal grows (COMLINE and TITCHEN, 1951).

As the rumen grows, it develops a fairly characteristic population of micro-organisms, bacteria and infusoria. The source of the infusoria is certainly by cross-inoculation from other animals, since none of the many species known can live outside the very highly specialized conditions of the rumen. If calves or lambs are kept in isolation, protozoa are never found in their rumens. Furthermore, by a combination of starvation and treatment with copper sulphate, it is possible to "defaunate" sheep, that is, to kill all infusoria inhabiting their rumens. If subsequently the sheep are kept in isolation and given normal feeds, no re-establishment of an infusorial population takes place. Contact for a time with normal sheep re-establishes the rumen infusoria. It is probable that cross-inoculation is of importance also in establishing some of the obligatory anaerobic bacteria which are found in the rumen.

The establishment of the rumen flora of calves has excited much attention recently and it has been suggested that inoculation of individuals with the cuds of ruminating cattle facilitates development of normal rumen function, possibly at an earlier age. These experiments have shown, however, that a rumen bacterial flora develops once solid food is supplied whether inoculations are given or not, which suggests that the ease of " infection " of the rumen with bacteria is considerably greater than the ease of infestation with protozoa. Nevertheless there is some evidence that inoculation gives rise to a greater diversity of

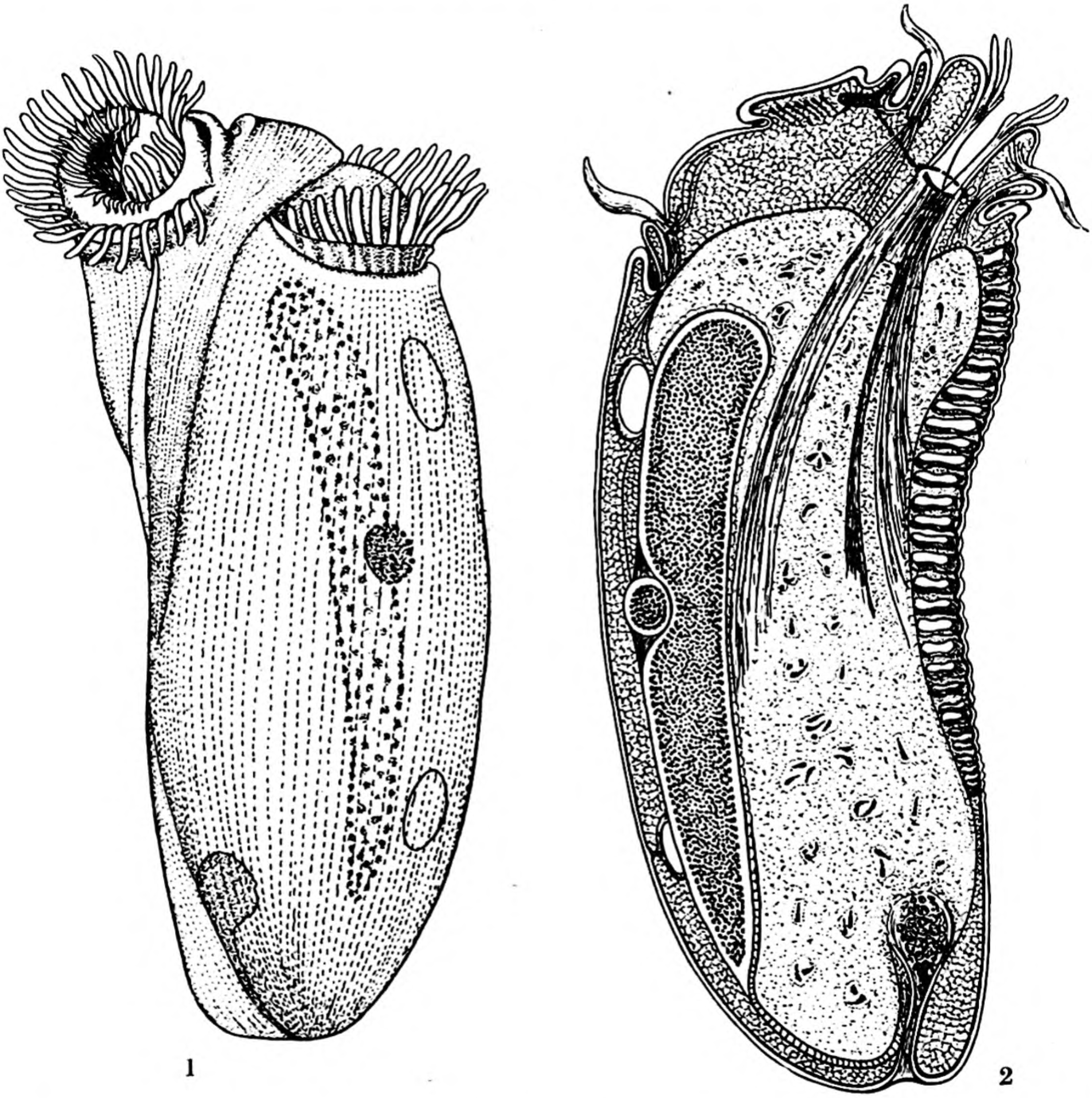


Figure 1.2. *Diplodinium ecaudatum* from the Stomach of Cattle (x ca. 1,000). (After Sharp, 1914.)

1. View of left side of body, showing macronucleus, micronucleus, contractile vacuoles, and other structures.
2. Median sagittal section, showing the structure of the extoplasm and endoplasm and the various fibrils which bring about retraction of the mouth region. The openings of the contractile vacuoles and the anus are shown.

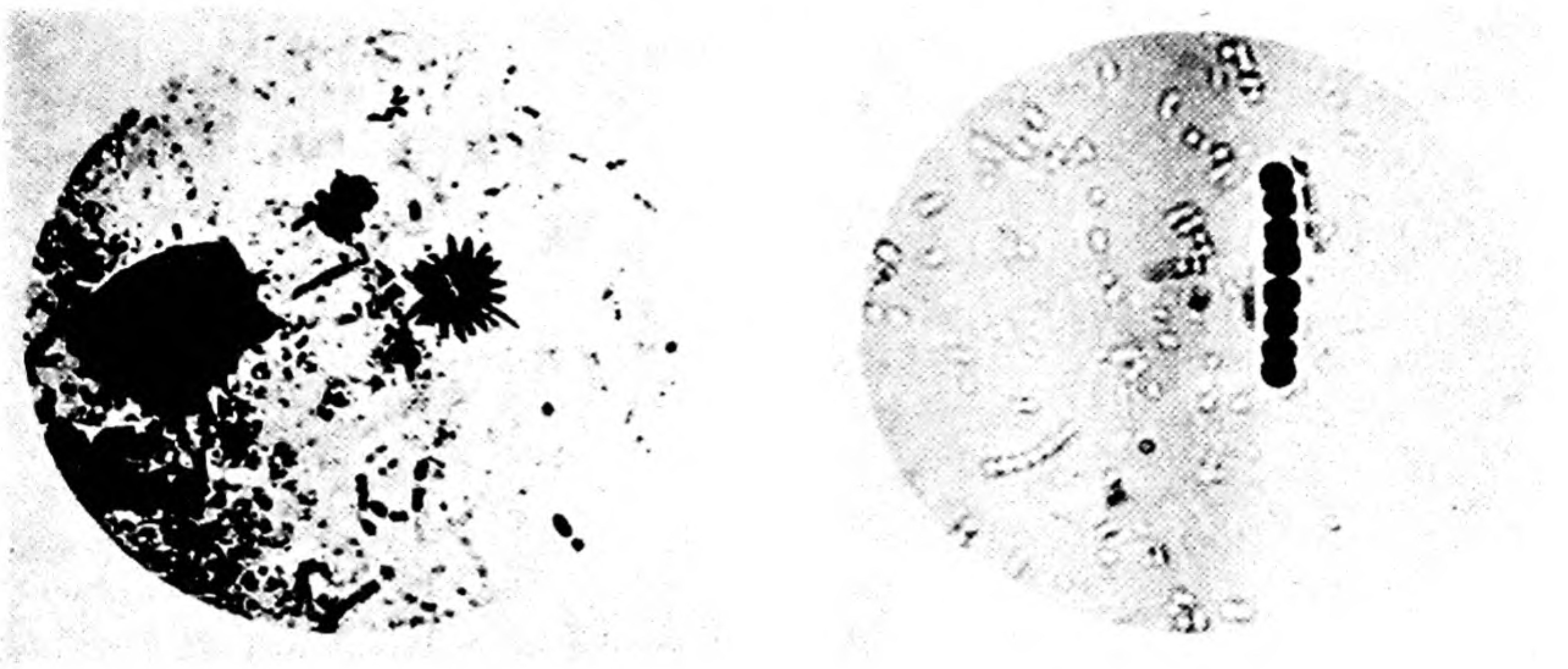
types and their more rapid establishment, but whether this is advantageous is not known (POUNDEN and HIBBS, 1948).

Since the flora and fauna of the rumen are of such importance, some remarks on the types of organisms present must be given. There are over 30 species of free-living infusoria known to be living in the rumen. Drawings of a common species are given in *Figure 1.2*, and it is common to find several species of a number of different genera inhabiting a single sheep or cow. Extremely large numbers of infusoria may be present. In grazing sheep in South Africa one cubic centimetre of rumen contents contains as many as four million individuals. They exhibit a considerable fluctuation in numbers, the variation being closely associated with the kind and amount of food entering the rumen (VAN DER WATH and MYBURGH, 1941). At present our knowledge of the factors concerned in the maintenance of populations of the obligatory anaerobic infusoria in the rumen is extremely meagre. Infusoria from the rumen cannot be multiplied *in vitro*. The role of infusoria in digestion is dealt with later.

As far as rumen bacteria are concerned, it must be remembered that this organ is subject to continual contamination from outside sources whenever food or water is swallowed. In fact it has been shown that aerobic organisms reach a peak of about 10^6 organisms per gramme directly after eating, but since conditions in the rumen are anaerobic these aerobes cannot easily become established (GALL and HUHTANEN, 1951). It is only organisms which can live and grow in the rumen which are of major importance in the digestion of feed.

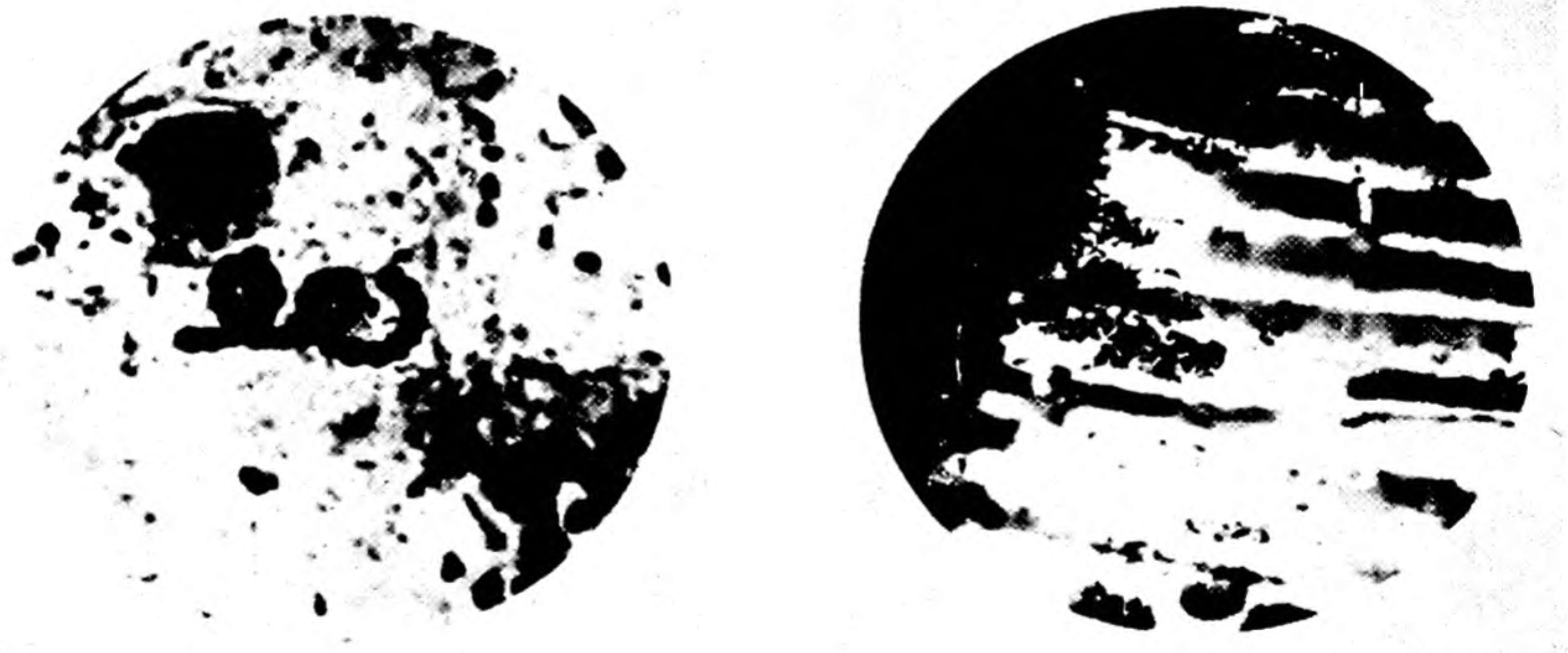
Direct slide counts of rumen organisms show that there are about 10^{11} anaerobes per gramme of contents. Their identification and classification is an extremely difficult task and some confusion in nomenclature already exists. A tentative scheme for the identification of rumen bacteria has been devised by MOIR and MASSON (1952). This is based on the appearance, staining reactions and ecological habitat of the bacteria, the latter term denoting particularly those organisms which are found in the fluid part of the rumen ingesta and those which are closely associated with fragments of plant material. Many of the rumen organisms are of rather striking shape, some taking the form of a giant star, others are kidney shaped, others spiral and still others best described as " window panes " (*Figure 1.3*).

Like infusoria, rumen bacteria show considerable changes in number and species dominance according to the type and amount of feed in the rumen. Some are slow-growing, others multiply rapidly. Some occur only under certain nutritive conditions and others appear commonplace. In all countries where they have been studied, marked seasonal variations have been found. It is extraordinarily difficult to evaluate quantitatively the role of individual species, and there is considerable evidence of a high degree of reciprocal dependence among several micro-organisms (BAKER and HARRIS, 1947–8). Many experiments have now been made, however, in which bacteria have been isolated from the rumen in pure culture, and their biochemical aptitudes examined. The results obtained are of considerable interest since they



Amylobacter radians

Amylococcus



Amylospinillum

Cellulose breakdown

Figure 1.3. Microphotographs of organisms inhabiting the rumen. The star-shaped rosette organism is probably organism no. 7 of Moir and Masson. Numerous free cocci and rods may be seen as well as chains. The photograph in the lower right corner shows the typical appearance of cellulosic material undergoing bacterial dissimilation. (*By courtesy of the late Dr. F. Baker.*)

reveal the complexity of the symbiosis which occurs. Direct culture from the rumen shows that fungi and "yeast-like" organisms are also present. An organism of the latter group has been studied intensively in South Africa where it may have some significance in the aetiology of bloat. Despite these massive changes in number, it was the opinion of Baker and Harris that the range of types present was qualitatively independent of the rations consumed.

In pigs and poultry, antibiotics included in the normal ration have led to enhanced food consumption and gain in weight. With ruminants in which the rumen flora is fully established, experiments have shown that the reverse is true. When, for instance, aureomycin was given to fattening steers, serious digestive disturbances occurred and the digestion of the carbohydrates of the feed was signally depressed (BELL, WHITEHAIR and GALLUP, 1951). Undoubtedly this was due to an interference with bacterial fermentation, since infusoria are not affected by most antibiotics. More direct evidence that antibiotics in the ration have deleterious effects on adult ruminants comes from studies in Australia where the feeding of aureomycin to sheep resulted in a fall in the number of micro-organisms in the rumen by 75 per cent. These could be restored by feeding rumen contents and yeast (TURNER and HODGETTS, 1952).

During the infantile stage in the growth of the ruminant, when the synthetic activity of the rumen flora is comparatively of small importance, there is evidence that antibiotics such as aureomycin, penicillin and terramycin do lead to increase in gain of body-weight. Part of this may be due to the effect of these antibiotics on the incidence of diarrhoea (scours), but bacteriological studies in young calves, as indeed in pigs and poultry, have not shown any consistent change in the numbers and types of organisms inhabiting the lower part of the intestinal tract. Experiments in which antibiotics have been given in the weaning period, namely when the rumen flora is beginning to establish itself, have given conflicting results and present knowledge suggests that the period during which antibiotics exert any favourable effect on food consumption or gain of body-weight is probably short.

The fact that in the infantile ruminant the characteristic rumen function of the adult is virtually non-existent makes it obvious that distinctions must be made between infantile and adult ruminant nutrition. In the pages which follow for ease of presentation the terms " lambs " and " calves " have been used in a rather more restricted sense than they are used in farming practice. Here they denote animals which have not been weaned and which have not developed a massive symbiotic flora in their rumens. Young ruminants which have been weaned and have developed a rumen microflora are referred to simply as " young cattle " and " young sheep ". For the adults, the usual agricultural terms are applicable. The collective terms employed are " suckling ruminant ", " young ruminant " and " adult ruminant " respectively.

NUTRITION OF THE SUCKLING RUMINANT

The first food of the ruminant animal is the thick yellow secretion of its mother, the colostrum. Since the time of EHRLICH it has been known that passive immunity to many infectious diseases is transmitted by the mother to the offspring, not only across the placenta, but also in the colostrum. The relative importance of the colostrum or the placenta in the transference of immunity depends largely on the complexity of the placental membranes separating the mother from the foetus. In the guinea-pig, where placentation in the late stages of pregnancy is of the haemo-endothelial type, no insuperable barrier is imposed to the passage of antibodies from mother to foetus, but in the cow, with its more complex syndesmochorial placenta, passage of large molecules is more difficult or in fact blocked, and passive immunity to infectious disease is transmitted almost entirely by the colostrum. The early studies of calf mortality by SMITH and LITTLE (1922) showed indeed that the acute intestinal infections of the calf were prevented by the ingestion of colostrum, while the studies of HOWE (1921) demonstrated that when colostrum was given to the calf, agglutinins for *Brucella abortus* appeared in the blood serum and were associated with a globulin fraction, precipitated by low concentrations of sodium sulphate or by saturated sodium chloride.

Recent work has confirmed and considerably extended these findings. Electrophoretic analysis of the serum of new-born calves has shown no γ globulin to be present, but that a slow-moving globulin appears following colostrum ingestion (SMITH, 1948). Furthermore, careful fractionation of the colostrum of the cow has demonstrated that immune bodies are closely associated with the lactoglobulin fraction, and that these appear in the blood (ASCHAFFENBURG *et al*, 1951). Nevertheless it appears that the lactoglobulins which the cow secretes in her colostrum and transfers to her calf are not identical with the γ globulin and so-called T component found in the serum of the adult bovine and there associated with immunity to infection. They differ in amino-acid composition, ultra-violet absorption spectra and in their physical properties. Though they are immunologically very closely related, they are not the same; in fact in calves which have been deprived of colostrum and yet survive, the slow manufacture of γ globulin can be followed, while in calves given colostrum the slow regression of the lactoglobulin component can also be measured.

Clearly, the resistance of the calf to many infections is closely associated with the immunity transferred in its first meal. With the fatal diarrhoea of calves associated with *Bact. coli* infection, colostrum containing agglutinins against the ' K ' antigens of the particular strains of *Bact. coli* concerned, afford protection. If the colostrum is deficient in agglutinins against the ' K ' antigens of the strains of *Bact.*

coli which are present, then no amount of it will prevent the death of the animal (BRIGGS *et al*, 1951).

With lambs given colostrum from ewes immunized against *Bact. typhosum,* it has been shown that absorption of the immune lactoglobulin carrying the antibodies can occur up to the 29th hour of life, but not after 48 hours. Similar time relations apply to the calf, and it is generally accepted that following 36 hours of extra-uterine life, absorption of intact protein molecules is impossible. The mode of absorption of these large protein molecules with mean molecular weights of about 180,000 has recently been studied at Cambridge. Experiments with new-born calves in which the thoracic lymph duct had been canulated, showed that introduction into the small intestine of colostral whey suitably labelled with agglutinins was promptly followed by a marked rise in the concentration of agglutinins in the lymph. With calves over 60 hours old no such rise was detected. In later experiments the antibodies and lactoglobulins were demonstrated in the lymph draining the intestine by the intestinal lymph trunk. It appears certain therefore that the unchanged lactoglobulins of colostrum do not enter the portal circulation but reach the peripheral blood *via* the intestinal lymph (COMLINE, ROBERTS and TITCHEN, 1951a). The protein, however, still has to enter the epithelial cells of the intestine, and histological studies have now shown that protein may be detected as globules in epithelial cells of the duodenum, jejunum and ileum of calves given colostrum early in life. In calves more than 60 hours old only a very small number of globules can be seen (COMLINE, ROBERTS and TITCHEN, 1951b). The factors controlling this ability of epithelial cells to absorb intact, protein molecules or perhaps particles are completely unknown.

While colostrum is of supreme importance in ensuring some degree of passive immunity for the new-born animal, its very richness in many vitamins and other dietary factors known to be essential for the growth of simple-stomached animals, suggests that it has a nutritional role to play no whit less important. Colostrum and milk are compared with regard to the more common dietary essentials in Table 1.1. The argument that the mere presence of a nutrient in an animal's natural diet thereby implies a physiological need for that nutrient is, however, extremely unsound and decidedly misleading. As an example of this may be cited the fact that sows' colostrum is particularly rich in ascorbic acid, yet attempts to demonstrate that the piglet requires any ascorbic acid, either at birth or subsequently, have failed ; in fact, on the contrary, the piglet is able to synthesize vitamin C from birth (BRAUDE, KON and PORTER, 1950). Similarly, cow colostrum and milk also contains an abundance of ascorbic acid and yet it is quite certain that at no time in its development does the calf require this vitamin. Even more striking evidence of the unsoundness of the assumption that milk or colostrum is necessarily completely adequate for the nutrition of the suckling is shown by the fact that when calves are given nothing but colostrum and milk for long periods, they develop anorexia, dyspnoea, nervous disturbances, rickets-like conditions, digestive failure and anaemia (HERMAN, 1936). Though a teleological explanation of the high concentration of certain vitamins in colostrum is attractive, it is certainly not necessarily correct.

TABLE 1.1

VITAMIN CONTENT OF COLOSTRUM AND WHOLE MILK

Vitamin	*Approximate quantity in*	
	Colostrum	*Whole Milk*
Vitamin A i.u./100 ml.	1,000–2,500[5]	200[5]
Vitamin E μg./g. fat	400[4]	50[4]
Aneurin μg./100 ml.	60–100[1]	30–40[1]
Riboflavin μg./100 ml.	350–750[1]	110–150[1]
Nicotinic acid	80–100[2]	80–100[2]
Pantothenic acid μg./100 ml.	200[2]	350[2]
Biotin μg./100 ml.	2–8[3]	2–8[3]
Folic acid	?	Trace only
Inositol	?	18
Ascorbic acid mg./100 ml.	200[6]	Falls in early lactation and rises again in late lactation.

[1] Houston, Kon and Thompson (1940)

[2] Pearson and Darnell (1946)

[3] Lawrence, Herrington and Maynard (1946)

[4] Blaxter, Brown and MacDonald (1953)

[5] Henry and Kon (1937)

[6] Rasmussen *et al* (1936)

In the last few years, however, a great amount of experimental study has been devoted to the specific requirements of the suckling ruminant animal. The methods used have been to provide liquid diets prepared from highly purified ingredients, and to exclude roughage from the diet entirely. In this manner, experiments may be carried out in which the development of the rumen flora and fauna is delayed, in fact in some experiments sulphonamide drugs and antibiotics have been included to reduce still further the activity of the gastro-intestinal flora. From such diets particular nutrients including vitamins of the B complex may be excluded with relative ease.

In some respects, these experiments with suckling ruminants given rations simulating milk, may be regarded as attempts to measure the nutrient requirements of the body proper of the ruminant. It is logical to assume that if the calf or lamb in which rumen function is negligible requires a particular member of the B complex, the adult animal will have a similar qualitative need which may be met by the synthetic activity of the micro-organisms inhabiting its rumen. It is possible that requirements are quantitatively much smaller in the adult than in the rapidly growing young. A further difficulty is that some nutrient requirements can at present only be measured in terms of the growth response they provoke.

As with simple-stomached animals, the studies using artificial diets for calves and lambs have revealed a dietary need for members of the vitamin B complex.

The most firmly established of these dietary requirements is that for riboflavin (vitamin B_2) which both the calf and lamb require in their diet. Riboflavin deficiency may be produced experimentally either by omitting it from an otherwise satisfactory artificial diet, or by giving as the sole diet cows' whole milk which has been subject to the rays of a mercury vapour lamp. In such "photolysed" milk, riboflavin is almost completely destroyed, and so incidentally is a considerable amount of pyridoxine. When a riboflavin deficient diet is given to calves one of the striking clinical signs is the excessive salivation and lachrymation which occurs. Appetite is generally poor and diarrhoea common (WIESE *et al*, 1947 ; WARNER and SUTTON, 1948). The clinical signs of the deficiency which have so far been described are not entirely in agreement with those observed in other species, most noticeable being the absence of marked changes in the retina of the eye. Nevertheless administration of riboflavin to deficient calves results in their recovery. With lambs riboflavin deficiency has been associated with loss of appetite and weight, leading to a terminal pneumonia (LUECKE *et al*, 1950; CULIK *et al*, 1949). Some attempts have been made to define the optimal requirement of the calf for riboflavin. The two estimates which have been made so far, differ by a factor of 3, part of which may be due to a breed difference (DRAPER and JOHNSON, 1952a; BRISSON and SUTTON, 1951). The estimates which lie between 1·0 and 4·0 mg. riboflavin per kg. dry feed consumed are, however, in reasonable agreement with an average value of 1·5 mg./kg. obtained with laboratory animals, and tend to indicate that the ruminant has no considerably greater requirement for this vitamin than have other species.

Other B-complex vitamins have also been studied using similar methods. Aneurin (vitamin B_1) appears to be required by both calf and lamb and a photograph of an affected lamb is given in *Figure 1.4*, but the evidence for other components is not yet entirely satisfactory. With nicotinic acid, no requirement was observed when calves were given rations containing adequate amounts of the amino-acid tryptophan, but if this amino acid was not supplied and the nicotinic acid content of the diet was simultaneously low, then deficiency signs—comparable to black tongue in the dog—developed. The conclusions which can be drawn at the present time from these types of experiments are tabulated in Table 1.2. Fat soluble vitamins are dealt with separately, since, apart from vitamin K, there is no evidence that the microflora of the gut plays any significant part in meeting the requirement of the tissues.

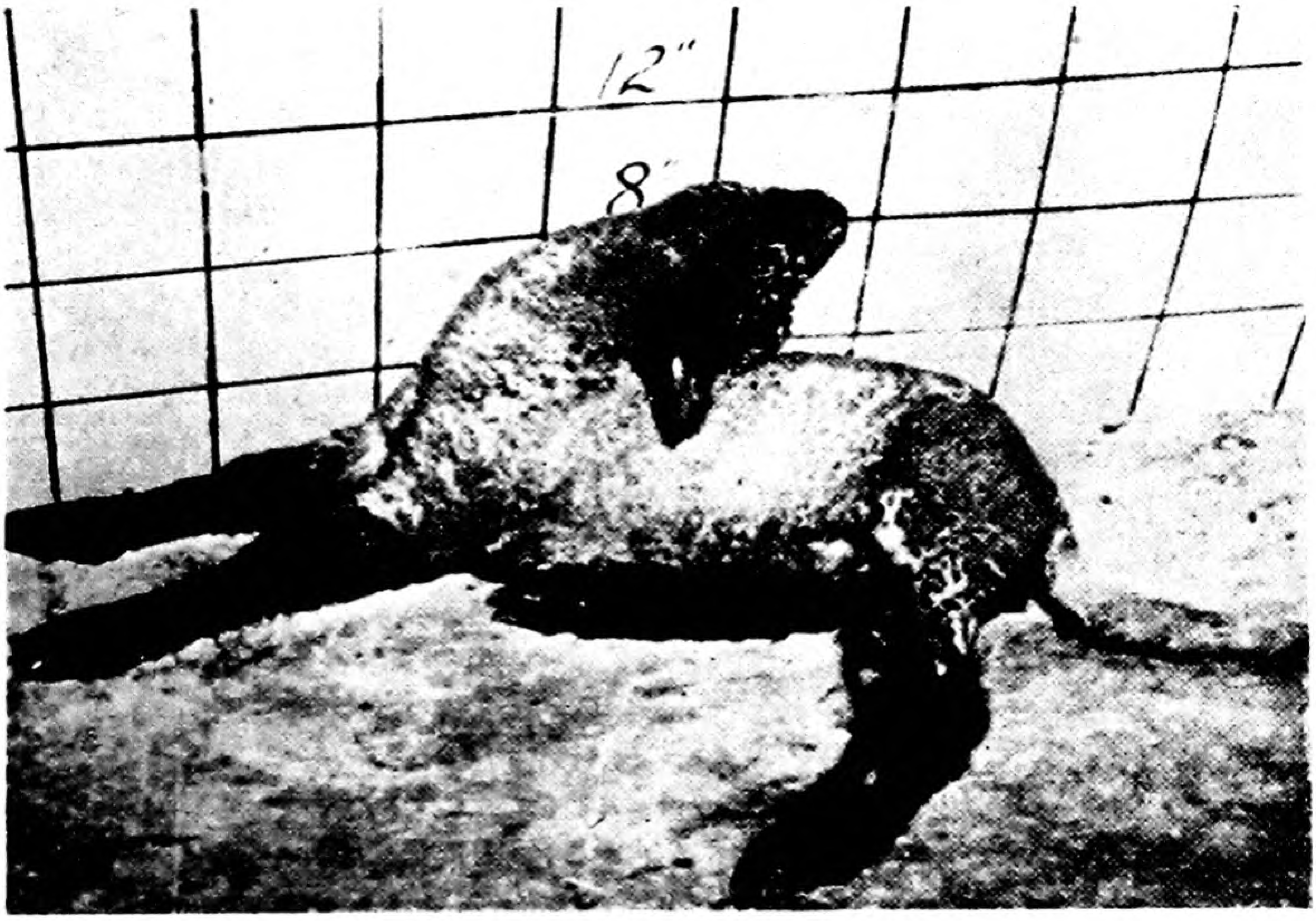


Figure 1.4. Vitamin B_1 deficiency signs in the lamb. The lamb was raised on an artificial diet free of aneurin. The neurological signs include marked postural defects, incoordination and opisthotonus.

Table 1.2 also presents the evidence that at present exists for the synthesis of vitamins by the adult microflora. In this respect it should be pointed out that many intestinal and other organisms may be shown to be capable of synthesizing severally or together all the known vitamins of the B complex. Conversely there are other organisms unable to synthesize these vitamins, in fact their inability to do so is made use of by employing them in the microbiological assay of vitamins. In the experiments carried out to provide evidence of synthesis, it has been usual to give rations to adult ruminants low in or free of a particular vitamin, and to determine the amount present in the rumen contents at a later time by abstracting some of the contents through a permanent fistula. Many of the vitamins increase so very markedly in concentration in the food mass during rumen fermentation, some as much as a hundred-fold, that it is inevitable to conclude that synthesis is taking place (KON and PORTER, 1947–8). Only with aneurin is the evidence for synthesis slight. It has been shown, however, that growing sheep and cattle can excrete unchanged in their urine and faeces more aneurin than they ingest with their food, so that it can be assumed that an overall synthesis does occur. Quantitative estimates of the amount of B-complex vitamins synthesized by the adult ruminant every day are extremely difficult to make, but it does appear that deficiency of a B complex vitamins can only be of rare occurrence and can in fact only occur as the result of grave disturbances of normal fermentative processes. An example of such a disturbance of synthesis of a B-complex vitamin is seen in cobalt deficiency of sheep and cattle. Cobalt is a structural part of the cobalamine nucleus of vitamin B_{12}, and the absence of cobalt from the ruminant's diet results in a failure of the microflora to synthesize the vitamin. The result is that the animal develops the alarming symptoms of the deficiency disease known as " pine " (MARSTON, 1952). Similarly, a blood abnormality of cattle characterized by a crinkling of the surface of the red blood cells (poikilocytosis) occurs if they are given abnormal diets of rice crispies and if they have open fistulae to their rumens (REID, HUFFMAN and DUNCAN, 1945). The disease appears due to a lack of pyridoxine in the body tissues.

As with vitamins of the B-complex, so with amino acids, the technique of the purified liquid diet has shown that the suckling ruminant requires certain dietary essentials preformed in its daily food. As will be discussed in detail later, the adult and growing ruminant obtains a significant part of its amino-acid supply following bacterial transformations of the nitrogen-containing compounds it ingests, so much so that some workers believe the adult subsists entirely on a ration of microbial protein. The suckling ruminant, however, requires some at least of the so-called 10 essential amino acids preformed in its diet. When, for instance calves are given rations containing casein as the sole source of protein, growth is not so satisfactory, nor is nitrogen retention so high, as when they are given the mixed proteins of cows' milk. When gelatin, a protein devoid of tryptophan and low in the sulphur-containing amino acids, is given, the animal cannot grow at all, loses weight, and, at the same time loses considerable quantities of nitrogenous metabolites in its urine (BLAXTER and WOOD, 1952a). With suckling calves dietary proteins may be classified in the same order of merit as they are in simple-stomached animals such as rats, dogs and man. This indicates that the body tissues of ruminants differ but little in nutrient requirement from those of other species, and once again demonstrates the significance of microbiological symbiosis in meeting the nutritional needs of the ruminant.

TABLE 1.2

EVIDENCE FOR VITAMIN SYNTHESIS IN THE RUMEN AND REQUIREMENT OF RUMINANT ANIMALS FOR VITAMINS

Vitamin	*Evidence for synthesis by micro-organisms in rumen*	*Evidence for a requirement of the vitamin by the host animal*
A	No—some evidence of very slight synthesis of carotene in the intestines of sheep[1]	Required even in the presence of an active rumen flora[9]
D	No[2]	Required even in the presence of an active rumen flora[10]
E	No	Required by the calf and lamb and by adult cattle[11]
K	Yes[3]	No evidence that it is required except in the presence of coumarins from spoiled sweet clover hay[12]
Aneurin	Yes, but probably only in small amounts[2]	Required by the calf and lamb, and some evidence that it is of importance in a rare disorder of Norwegian cattle [13,14]
Riboflavin	Yes[3]	Required by both calf and lamb (see text)
Nicotinic acid	Yes[4]	Not essential when ration rich in tryptophan, but requirement can be demonstrated in the absence of tryptophan[15,16]

[1] McGillivray (1951)
[2] Kon and Porter (1947-8)
[3] McElroy and Goss (1940)
[4] Wegner *et al* (1940)
[5] McElroy and Goss (1939)
[6] Lardinois *et al* (1944)
[7] Porter (1953)
[8] Knight *et al* (1940)
[9] Hart (1940)
[10] Rosenberg (1945)
[11] Blaxter and Brown (1952-3)
[12] Link (1944)

ADULT NUTRITION—ENERGY METABOLISM AND REQUIREMENTS

Though emphasis has so far been given to the importance of vitamins and specific amino acids as dietary essentials in the ration of suckling ruminants, it would be very wrong to conclude that these are of major importance under practical conditions. Many deficiency states can only be produced under very rigorous experimental conditions, in which abnormal diets are given for long periods and the normal weaning period is considerably postponed. They have been cited more to show the importance of the rumen microflora in meeting the tissue requirements of the animal than as demonstrations that the suckling animal may suffer from deficiency under practical conditions. Conceivably it could if milk substitutes deficient in these factors were ever employed

TABLE 1.2 (*Continued*)

EVIDENCE FOR VITAMIN SYNTHESIS IN THE RUMEN AND REQUIREMENT OF RUMINANT ANIMALS FOR VITAMINS

Vitamin	*Evidence for synthesis by micro-organisms in rumen*	*Evidence for a requirement of the vitamin by the host animal*
Pyridoxine	Yes[5]	Shown by American workers to be essential for the calf. Is involved in poikilocytosis of cattle observed in North America[17]
Biotin	Yes[4]	Claimed by American workers to be essential for the calf, but claim not substantiated in more critical British experiments[18, 19]
Pantothenic acid	Yes[5]	Claimed by American workers to be essential[20]
Choline	?	Claimed by American workers to be essential if diets low in methionine are given[21]
Inositol	Not known, but highly probable[2]	Not known
Folic acid	Yes[6]	Deficiency produced by using folic acid antagonists in lambs[22]
B_{12}	Yes[7]	Shown to be required by sheep deficient in cobalt[23]
Ascorbic acid	Destroyed in the rumen[6]	Not required at any age

[13] Johnson *et al* (1948)
[14] Draper and Johnson (1951)
[15] Johnson *et al* (1947)
[16] Blaxter and Wood (1952a)
[17] Johnson, Pinkos and Burke (1950)
[18] Wiese, Johnson and Nevens (1946)
[19] Kon and Porter (1951)
[20] Johnson, Mitchell and Hamilton (1947)
[21] Johnson, Mitchell and Pinkos (1951)
[22] Draper and Johnson (1952b)
[23] Smith, Koch and Turk (1951), Marston (1952)

widely, but even so, signs of malnutrition with respect to energy supply would probably appear first. It has been very rightly concluded by HUFFMAN and DUNCAN (1945) that of all the naturally occurring nutrient deficiencies which affect the productivity of farm livestock, shortages of dietary energy is primary, and that, compared with these shortages, deficiencies of vitamins and mineral elements, though still of importance in isolated instances, occupy a very secondary place. This is so whatever age the animal may be, and the study of the need for dietary energy on the part of ruminants, and the complex means whereby the adult obtains a source of energy from the cellulosic materials of its feed, continues to be the main preoccupation of many who are concerned with ruminant nutrition.

Table 1.3 compares the fate of dietary energy in a suckling calf and in an adult sheep, animals of approximately the same size.

TABLE 1.3

THE ENERGY EXCHANGE OF THE SUCKLING AND THE ADULT RUMINANT

	Calf given 4 l. cow's milk[1]	*Sheep given 826 g. dry feed*[2]
Weight of animal (Kg.)	35·1	45·0
Calorie intake per day	2,979	3,626
Calories lost in faeces	58	1,270
" " " urine	120	234
" " " methane	0	224
Calories " available to the animal "	2,801	1,898
Calories lost as heat	2,071	1,557
Calories stored as fat and protein in the tissues	730	341

[1] Blaxter (1952) [2] Heinzl (1944)

Table 1.3 shows that whereas the young calf loses negligible amounts of dietary energy in its faeces and urine and none as methane, the sheep when given its normal diet, loses nearly 50 per cent of the energy of its feed by these routes. The faeces represent the major channel of loss. The loss of heat by the calf, however, is considerably greater than the loss of heat by the sheep. To interpret these observations more closely it is necessary to consider how the results of such experiments may best be presented in a schematic fashion. It is usual to denote the number of Calories which are not lost to the animal in visible excreta or combustible gas as metabolizable energy. The energy which the animal deposits in its body tissues is termed net energy. The latter obviously varied with the level of feeding. Expressing this relationship in terms of an equation we have :

$$\text{Energy stored} = a\,(\text{metabolizable energy}) - b'$$
$$i.e. \quad EB = a(ME) - b'$$

The constant (a) in this equation denotes the fraction of metabolizable energy which is realized as net energy, while the constant (b') represents the energy balance of the animal when it ingests no feed, namely the " minimum base value of heat production " (FORBES and SWIFT, 1941). This value (b') is an approximation to the animal's basal metabolism, though in fact basal metabolism is higher because it measures not solely the minimum metabolism of the tissues but also the energy the animal expends in catabolizing body substance to meet these minimal demands. To equate for differences in body size, which would affect the magnitude of b' above, the equation can be expressed in units of metabolic body size (BRODY, 1945), that is body weight

" W " raised to the power 0·73 *viz.*

$$\frac{EB}{W^{0\cdot73}} = a\,\frac{ME}{W^{0\cdot73}} + b$$

Then b will represent the minimum base value of heat production of one unit of metabolic body size, that is per kg. of weight raised to the power 0·73. The significance of the constant a is unaltered. The data of Table 1.3 may now be expressed in accordance with these conventions.

First it is evident that the calf has a very considerably greater requirement of energy for maintaining itself, double that required by the adult sheep, an animal of the same size. The higher metabolism of the young animal has long been realized, but in the past it was usual to suppose that per unit of surface area, to which metabolic body size is fairly closely related, metabolic rates of young and old animals differed but slightly. Obviously these results are of importance in deciding the energy allowances to be given to the young animal.

TABLE 1.4

THE UTILIZATION OF DIETARY ENERGY BY THE SUCKLING CALF AND BY THE ADULT SHEEP AND OX

	Suckling	*Adult*	*Adult*
	Calf *Milk*[1]	*Sheep* *High quality fodder*[2]	*Ox* *Low quality fodder*[3]
Maintenance requirement per kg. of metabolic body size Cals./day	121·6	54·6	51·9
% of metabolizable energy available for body gain	85	62	50
% of metabolizable energy lost as heat	15	38	50
% of gross energy metabolizable	95	70	55
% of gross energy of real value, *i.e.* realized as net energy	79	43	28

[1] Blaxter (1952) [2] Marston (1948) [3] Forbes *et al* (1930)

What is more striking, however, is that in the adult a considerable part of the dietary energy, which remains after all urinary, faecal and gaseous losses have been accounted for, is dissipated as heat and serves no useful productive function in the body. The loss by the calf of 15 per cent of the metabolizable energy of its feed as heat is exactly comparable to the losses which occur in similar experiments with man, dogs, rats and mice, that is, animals with simple stomachs (LUSK, 1928). It is only with ruminants that losses of heat amounting to 30–50 per cent of the metabolizable energy take place. These losses represent one of the taxes on the animal's economy which the ruminant life imposes. Many experiments, dating from the time of **Kellner** have shown that the heat lost per unit of metabolizable energy varies with the type of food. It is maximal with foods which are high in " fibre " content and minimal with those which are low. **Breirem** (1944) in Norway, by analysis of published European and American experiments with cattle, found that the net availability of metabolizable energy (the constant a in the equation above) was related to the crude fibre content of the food by the equation:

$$100a = 65{\cdot}6 - 0{\cdot}70 \times \% \text{ of crude fibre in the feed.}$$

This equation, which has a fairly wide error attached to it, implies that even if cattle were given rations free of fibre, or at least low in fibre, comparable in fact to human dietaries, they would still utilize about 66 per cent only of the metabolizable energy contained therein. The better utilization of energy by the suckling calf compared with the adult cannot thus be explained solely on the basis of the fibrous nature of the normal feed of the adult. If this were so, one would expect the intercept of the equation to be a value approaching 85 per cent. Nevertheless, the utilization of the cellulosic portions of the ruminant's feed does appear to involve an additional expenditure of energy, as was shown in the classical studies of Kellner many years ago. Why this is so has not yet been ascertained, but considerable advances have been made recently in our knowledge of the events which occur in the rumen when cellulosic materials are being degraded.

With the exception of the snail, no animal secretes in its digestive juices any enzyme capable of hydrolysing cellulose. Cellulose digestion takes place as the result of the action of bacterial cellulases in places where the passage of food through the digestive tract is delayed, such as the rumen of ruminants, the large intestine of the horse and the caecum of the rabbit (**Phillipson**, 1947–8). The passage of foodstuffs through the alimentary tract of the ruminant is a slow process. It takes about 7–10 days for the complete passage of a single meal through the digestive tract, longer for coarse fodders than for more concentrated foods. The delay in the rumen has been estimated to be approximately 70–90 hours (**Balch**, 1950). This does not mean that following a meal no ingesta leave the rumen until that length of time has elapsed, nor does the figure of 7–10 days mean that this is the normal rate of flow of ingesta past a single point in the digestive tract. Studies with sheep have shown that ingesta passes through the abomasum in gushes at intervals of less than 15 minutes, while calculations from studies with cows leave little doubt that the passage of digesta from the rumen is relatively continuous over the 24 hours, being controlled by the valve-like action of the omasum and the sharp contractions of the reticulum. The amounts leaving at any one time are, however, small, and since there tends to be separation of the ingesta in the rumen dependent upon the degree of comminution of food particles. The most recently digested feed particles which are larger and lighter tend to remain in the rumen for a long period. As far as the physical events are concerned, rumen function is thus a complex continuous process and there is never the clear demarcation of ingesta as with simple-stomached animals. The vigorous contractions of the rumen and reticulum (SCHALK and AMADON, 1928), the process of regurgitation and rumination, all contribute to the mixing of ingesta from individual meals.

It has been estimated that during sojourn in the rumen, approximately 70–85 per cent of the digestible dry matter of the ration disappears (GRAY, 1947). The fermentations in the rumen clearly overshadow entirely the rest of digestion in the alimentary tract.

Quantitatively of considerable importance in the diet of ruminants are the fibrous components of feeds, cellulose, lignins, hemicelluloses and encrusting polyuronides. In 1884 it was shown by TAPPEINER that bacterial fermentation of cellulose in the rumen of the ox resulted in the formation of large amounts of steam volatile fatty acids, and he concluded that the mixture contained at least 50 per cent acetic acid. This finding was confirmed in the later part of the last century, but investigators were unwilling to accept the implications of the results, since at the time they did not seem compatible with the calorimetric observations of Kellner which ascribed to digested cellulose a nutritive value equal to that of digested starch. Attempts were made to show that glucose was a normal intermediary in the digestion of cellulose. It is now known that cellulose, starch and glucose give rise to a high proportion of fatty acids. In this respect there is considerable evidence that during bacterial fermentation in the rumen, bacterial polysaccharide is formed as the bacteria proliferate. Similarly the holotrich ciliates from the rumen are able to build up iodophilic polysaccharide granules in their bodies from fructose, inulin, bacterial levans and to a lesser extent cellobiose (MASSON and OXFORD, 1951). The quantitative importance of this potential source of hexose in the animal's economy is however unknown, but in any case is quantitatively small compared with the energy which is liberated in the rumen as steam volatile fatty acids. Final proof of the importance of volatile fatty acids in ruminant metabolism came from studies at Cambridge by BARCROFT, PHILLIPSON, ELSDEN and others. These workers confirmed the presence of the acids in the rumen, demonstrated their absorption into the portal blood, and settled many of the outstanding questions left unanswered since the time of TAPPEINER's first observations.

There is considerable evidence that the concentration of the volatile fatty acids, and of lactic acid in the rumen is dependent upon the nature of the feeding stuff being fermented (PHILLIPSON, 1942). The concentration of total steam volatile fatty acids per 100 ml. varies from

0·2–1·2 g./100 ml., while the concentration of lactic acid varies considerably from an undetectable amount to 10 mg. equiv./100 ml. In terms of total quantity present at any one time, it has been found that the whole rumen of the sheep contains volatile acid equivalent to 64 g. acetic acid and the rumen of the ox 286–371 g. of volatile acid. These values for concentration of volatile fatty acid cannot indicate the total daily turn-over, since fermentation and absorption of the products are parallel processes. Some idea of the time-relationships of concentration of volatile acids and lactic acid in a sheep given glucose are, however, shown in *Figure 1.5* (ELSDEN, 1945).

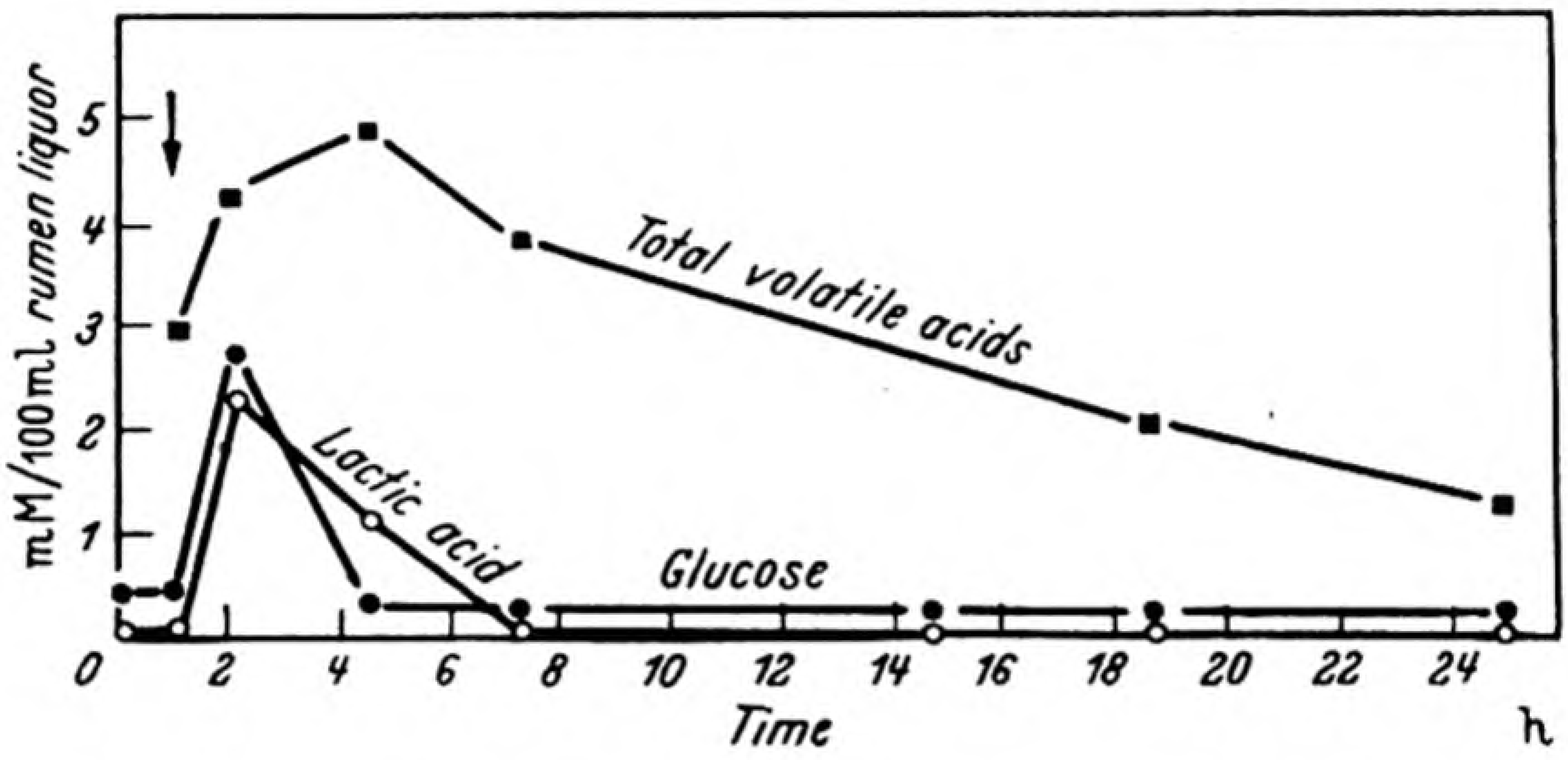


Figure 1.5. The effect of introducing glucose into the rumen of the sheep. A rapid rise in the lactic acid concentration takes place coinciding with the fall in glucose concentration. The steam volatile fatty acids also increase in concentration. In this experiment schizosaccharomycetes (Quin's organism) increased in number and clearly were storing considerable amounts of a polysaccharide. The iodophilic cocci which are normally present in very large numbers had clearly been supplanted by this organism (Elsden, 1945. By courtesy, *J. exp. Biol.*).

Steam volatile acids produced in the rumen consist in the main of acetic, propionic and butyric acids. Small amounts of higher fatty acids (valeric and hexanoic), possibly amounting to about 3 per cent of the total, are also present (MCCLYMONT, 1951) and small amounts of formic acid may be found as well. Table 1.5 shows the percentage of acetic, propionic and butyric acids in the total steam volatile acids which can be isolated from the rumens of sheep given different—but not widely different rations.

It will be noted that the composition of the mixture of fatty acids in the rumen varies with diet. Starchy diets appear to favour a large proportion of propionic acid and also incidentally a large concentration of lactic acid, as can in fact be inferred from *Figure 1.5*. Mangold feeding also favours lactic acid appearance, but normally lactate seldom accumulates in any quantity: it decreases as rapidly as it is formed.

TABLE 1.5

PERCENTAGE DISTRIBUTION OF THE STEAM VOLATILE FATTY ACIDS PRESENT IN THE RUMENS OF SHEEP 2 HOURS AFTER FEEDING

	Wheat hay[1]	*Lucerne hay*[1]	*Hay + maize*[2]	*Hay + linseed + blood meal*[3]
Acetic	59	70	37	75
Propionic	35	19	48	16
Butyric	15	11	12	9
Higher	Not recorded	Not recorded	3	Not recorded

[1] Gray and Pilgrim (1951) [2] Phillipson (1952b) [3] Schambye and Phillipson (1949)

Obviously, the mixture of acids which is present in the rumen are not necessarily the same as the mixture which is produced by fermentation. One method of studying the amounts formed, and indeed the whole course of the fermentation, is to study the fermentation *in vitro* under carefully controlled conditions. Such experiments have been made by many workers, notably by MARSTON (1948) who devised an artificial rumen in which cellulose was fermented by the mixed organisms from the rumen of sheep under conditions comparable to those of the normal sheep. Typical results are given in Table 1.6.

TABLE 1.6

THE FATE OF THE COMBUSTIBLE ENERGY OF CELLULOSE DURING FERMENTATION IN THE RUMEN (MARSTON, 1948)

		Kg. Cal.
Amount of cellulose digested		100
Volatile acids produced:	formic	0·1
	acetic	18·5
	propionic	57·5
	butyric	1·6
Methane produced		7·9
Micro-organisms produced (growth)		8·0
Lost as heat		6·0

What is of interest in these studies is that whereas in the rumen acetic acid generally predominates, in this fermentation *in vitro* propionic acid appeared to be the main end product (molar ratio propionic/acetic = 1·8). Acetic acid arises in the rumen not only from cellulose, but also from sugars and hexosans as well as from amino acids. It is possible that under certain conditions propionic acid will predominate, but normally acetic acid will be present in the highest concentration. There is overwhelming evidence that the steam volatile acids are absorbed through the rumen wall, as are indeed many other substances. This is remarkable, since the wall of the rumen is covered with a cornified epithelium. The critical test of demonstrating the presence of acetic acid in the blood draining the isolated rumen leaves no doubt that, despite its appearance, the rumen wall is permeable (DANIELLI *et al*, 1945; GRAY and PILGRIM, 1951; PHILLIPSON, 1952a). Acetic acid appears to be absorbed faster than the other fatty acids under normal physiological conditions.

The whole question of the interpretation of the concentrations of steam volatile acids in the rumen is rendered even more complicated, however, by the fact that the rumen epithelium of the sheep can metabolize butyric and to a lesser extent acetic and propionic acids resulting in the production of ketone bodies (PENNINGTON, 1952).

Not all the steam volatile acid is absorbed from the rumen. A large part flows with the digesta into the abomasum and small intestine. Its concentration there is small and this is presumptive evidence that it is absorbed, in fact the estimate of 1–5 g. of steam volatile acid absorbed per hour by the sheep may be too low by a factor of 3 to 5.

It is therefore quite clear that quantitatively the volatile acids are a major product of cellulose digestion. From Table 1.6 it may be seen that the 100 Calories of cellulose digested gave rise to only 6 Calories of heat due to bacterial fermentation and 8 Calories as methane. If acetic acid and propionic acid entered the cycles of intermediary metabolism with a loss of energy comparable to that undergone by glucose in animals with simple stomachs, then, from these results, it may be calculated that the productive value of cellulose would be about 85 per cent of its metabolizable energy. It has already been pointed out that the net energy value of the ruminant's food is about 50 per cent of the metabolizable energy. To reconcile these two results, one can only conclude that the utilization of the lower steam volatile fatty acids is associated with an appreciable loss of energy as heat. The metabolism of propionic acid presents no difficulties to the animal, but with acetic acid, though it is thought to be of primary importance in certain intermediary transferences as "active acetate", it is not necessarily easily diverted into productive channels. That acetic acid may apparently be used by animal tissues as a source of energy—for the maintenance of the heart beat for instance (BARCROFT, MCANALLY and PHILLIPSON, 1943)—has been established, and that it disappears from arterial blood during passage through the tissues of the head has also been shown (REID, 1950). Furthermore, studies with acetic acid labelled with radioactive carbon have demonstrated without any doubt that acetic acid plays a significant part in the synthesis of the fatty acids of milk fat, probably some 40 per cent of the fatty acids of milk arising from stepwise synthesis from steam volatile acids (FOLLEY, 1952). What remains unknown are the thermodynamic losses involved in the utilization of volatile acids in sparing tissue destruction during starvation and in promoting storage of energy in the body as fat.

The physical processes in the rumen which ensure a thorough trituration of the food mass and are concerned in its passage have already been discussed. Equally important are the physiological adjustments which ensure that the chemical conditions in the rumen contents are ideal for the rapid proliferation of bacteria. The *p*H of the rumen varies between limits of 7·5 and 5·8. Alkaline conditions occur as the result of starvation in most instances, though South African studies suggest that they occur also following feeding on certain mature hays. The most highly acid conditions follow the rapid fermentation of sugars or foods rich in sugars, and the lowest value obtained occurs about four hours after a meal (Phillipson, 1942). The fluid contents of the rumen are heavily buffered, so that the large changes in volatile acid have relatively small effects on the *p*H. The buffering systems in the rumen, for there are many, are complex. Strong bases of the food and ammonia arising from bacterial degradation of protein in the rumen together with the weak volatile acids undoubtedly form one. Others are due to phosphates in the food and saliva and to soluble proteins with weak charges. One extremely important system is the bicarbonate system, which arises from the salivary bicarbonate and the carbon dioxide arising from bacterial action. This involves also a consideration of the gas phase of the rumen.

The salivary secretion of the ruminant, relative to its size, is immense. It has been estimated in the ox to be some 50–60 litres daily, while recent experiments with sheep indicate that a single parotid salivary gland can secrete up to 1,840 ml. per day (McDougall, 1948). For comparison, man secretes about 1·5 litres of saliva in a day. The composition of sheep saliva is compared with sheep serum in Table 1.7.

TABLE 1.7

THE COMPOSITION OF PAROTID SALIVA AND OF SERUM IN THE SHEEP

	Parotid saliva	*Serum*
Total solids (g./100 ml.)	1·3	8·3
Nitrogen (mg./100 ml.)	20	865
Sugar ,,	0	105
Na ,,	408	365
K ,,	32	35
Ca ,,	0·8	10
Mg ,,	0·8	2
Inorganic P ,,	81	5
Cl ,,	61	370
CO_2 (ml./100 ml.)	233	56

Outstanding is the fact that the total CO_2 content is extremely high and so is the phosphate. It may be calculated that the sheep secretes daily some 2·7 equivalents of bicarbonate, while in the rumen at the peak of fermentation there is about 1·1 equivalents of volatile acid. Obviously the bicarbonate and phosphate of saliva have an extremely important role in maintaining the rumen fluid as an ideal buffered medium for the growth of micro-organisms.

The gas phase of the rumen undergoes cyclical changes coinciding with the ingestion and bacterial fermentation of food. The O_2 content is always extremely small, the maximum concentration being present immediately after eating. The fermentation produces massive quantities of CO_2, some arising from the fermentation phase (10 litres per 100 g. cellulose digested) and some from the partial neutralization of the volatile acids produced. Methane is also produced in fairly large quantities—about 3·5 litres per 100 g. cellulose digested. Hydrogen is also produced in the rumen but in normally fed animals it is rarely detected. It is thought that methane arises by the reduction of CO_2 by H_2 produced in simultaneous fermentations, and that it is only abnormal conditions such as starvation that uncouple the two processes of H_2 production and CO_2 reduction with the result that H_2 accumulates (PILGRIM, 1948). Other gases, notably H_2S, have been detected in the rumen, the latter probably arising from decomposition of sulphur containing amino acids.

Much of the gas produced in the fermentation is lost by eructation, but a large amount of the CO_2 and to a lesser extent the methane is absorbed and excreted by way of the lungs. As the fermentation reaches completion, CO_2 tends to become markedly reduced in concentration since it diffuses quickly into the blood, while N_2 tends to accumulate. The composition of the gas mixture in the rumen is thus by no means constant. Table 1.8 gives average results obtained at various times after a single meal of grass (BRODY, 1945).

TABLE 1.8

COMPOSITION OF THE GAS PHASE OF THE RUMEN

Percentage by volume

	Immediately after eating	*At height of fermentation (4 hr. later)*	*24 hours after the meal*
Oxygen	5	0	0
Nitrogen	15	1	35
Carbon dioxide	55	70	20
Methane	25	29	45

The increase in CO_2 production following upon a meal can be responsible for " bloating " of cattle. " Bloating " is due to gas accumulating in the rumen with consequent increase in intra-abdominal pressure and death (COLE *et al*, 1945). The reasons why the normal processes of eructation are not sufficient to deal with excessive gas production are not known. In some instances, when the gas bubbles become entrapped in the ingesta (" frothy bloat ") eructation would be of little avail, but in others it appears that there is some interference with the normal process of eructation. This may be due to toxic factors in the food (FERGUSON *et al*, 1949) or to rumen atony. Substances which reduce surface activity, such as turpentine and polymerized silicones, are effective in the treatment of frothy bloat.

ADULT NUTRITION—PROTEIN METABOLISM AND REQUIREMENTS

The important part played by the rumen flora in the nutritional physiology of the ruminant animal is not limited to the utilization of the energy-yielding constituents: it applies equally well to the nitrogen-containing moieties.

The utilization of dietary protein, or more correctly, dietary nitrogen, is usually estimated by methods involving the analysis of food and excreta and the computation of the storage—or loss—of nitrogen which occurs on a particular dietary regimen. From such information it is possible to compute the " biological value " of the nitrogen-containing parts of the diet, that is, their ability to provide a source of amino acids to be used for meeting the inevitable losses of body constituents containing nitrogen and providing for the synthesis of new tissue in growth or the proteins of milk and wool (MITCHELL, 1943). In simple-stomached animals, such as man and the rat, and indeed the suckling calf, biological values vary widely according to the amino-acid composition of the protein which is consumed. Thus the proteins of whole egg have a biological value of 100; casein, which is low in the sulphur-containing amino acid, methionine, has a biological value of approximately 70, while gelatin has a biological value of less than 30.

With ruminant animals, differences in biological value of different dietary proteins are very small. Proteins which in rats are much superior, in sheep do not appear very much better than poor sources of amino acids. In fact, some workers have concluded that there are no differences at all in the biological value of dietary sources of nitrogen for ruminants. This conclusion is supported by the fact that simple nitrogen containing materials such as urea and ammonium salts can support nitrogen retention in ruminants, whereas in animals with simple stomachs they are completely valueless as a sole source of nitrogen (MCNAUGHT and SMITH, 1947–8).

The extent of variation in the biological value of dietary protein in ruminants is given in Table 1.9.

The data in Table 1.9 show that averages of biological values of proteins tend to be about 75 in cows and about 60 in sheep. This apparent difference in nitrogen utilization as between species will be commented on later. The differences between proteins were found to be negligible. Thus with sheep it was found that casein has almost the same biological value as urea when the level of substitution of urea for casein was equivalent to 10 per cent of crude protein in the ration. At higher levels of substitution urea appears to be less useful (HAMILTON *et al*, 1948).

TABLE 1.9

THE MEAN BIOLOGICAL VALUE OF DIETARY PROTEIN IN RUMINANTS

Animal	*Function*	*No. of determinations*	*Mean biological value and its standard deviation*
Cow*	Milk production[1]	70	75·3 ± 7·3
Cow*	Milk production[2]	58	74·1 ± 7·6
Heifer	Growth[3]	24	74·8 ± 4·6
Sheep	Growth[4]	325	62·0
Sheep	Growth[5]	14	60·8 ± 2·4

[1] Morris and Wright (1933) [2] Hart and Humphrey (1916) [3] Swanson *et al* (1943)
[4] Miller and Morrison (1942) [5] Johnson *et al* (1942)
* The values for milking cows are not those published by the authors, but are the result of a recalculation of their data.

Obviously, the facts that, firstly, adult or growing ruminant animals can live on rations devoid of amino acids provided that a source of nitrogen is supplied as urea and, secondly, the suckling one clearly needs a dietary source of amino acids, mean that the rumen microflora dominates protein metabolism in much the same way that it dominates energy metabolism. An elegant demonstration of the importance of the rumen in modifying the nutritive value of dietary protein has been made by CUTHBERTSON and CHALMERS (1950). These workers measured the nitrogen retention of sheep when given casein either through a fistula into the rumen or through a cannula inserted in the duodenum, the latter, of course, by-passing the rumen. When the casein entered the rumen the retention by the sheep of the nitrogen it contained was considerably smaller than when the casein was inserted in the duodenum and micro-biological activity in the rumen avoided. It is clear then that not only do simple nitrogenous materials show an enhanced nutritive value in ruminants, but that proteins accepted as of high quality are under some conditions degraded.

It has already been seen that the fermentation of carbohydrates in the rumen involves a considerable growth of the rumen bacteria, and, as first suggested by ZUNTZ many years ago, the utilization of non-protein nitrogen by ruminants can be accounted for by its conversion to the proteins of micro-organisms and the subsequent digestion of this microbial protein lower in the digestive tract. Much evidence has accrued in recent years to suggest that Zuntz's hypothesis is correct in its broad essentials, but at the same time it has been shown that the nitrogen metabolism of the rumen is of considerable complexity, and that other factors have to be considered as well.

As with studies of carbohydrate utilization both *in vivo* and *in vitro*, experiments have been made to study the synthesis and degradation of protein in the rumen.

The first stage in the utilization of protein or simple non-protein nitrogenous compounds in the rumen is the liberation of ammonia. When casein is introduced into the rumen for instance, the concentration of ammonia rises immediately, reaches a peak in two hours and then declines (McDonald, 1952). With urea utilization, it has been shown that the rumen contains a very potent urease sufficient to convert all the urea ever likely to be given to a cow into ammonia within an hour (Pearson and Smith, 1943a). Coincident with this rise in the ammonia content of the rumen fluid, the ammonia content of the venous blood draining the rumen rises (McDonald, 1948a). Undoubtedly a greater part of this ammonia is converted into urea in the liver of the ruminant. Certainly it does not accumulate in the blood since it is toxic in relatively small concentrations. Some of the urea reaches the rumen again as urea from the saliva, almost all the nitrogen of saliva being accounted for by urea (McDonald, 1948a). Some, however, is excreted by the kidneys, and this accounts for part at least of the rise in urinary nitrogen excretion when casein is introduced into the rumen compared with when it is introduced into the duodenum.

De-amination of the constituent amino acids of proteins in the rumen produces ammonia and carbon-containing fragments. These are not the corresponding keto acids which occur when amino acids are oxidatively de-aminated, nor the corresponding hydroxy acids which occur on direct hydrolysis. El Shazly (1952) has shown that the main reaction products of bacterial de-amination are ammonia, carbon dioxide and steam volatile fatty acid, in roughly equimolecular proportions. The steam volatile acids produced are of considerable interest since they consist of both straight and branched chain acids in the series C_2 to C_5. Acetic acid predominates, but the branched chain acids are of particular interest since they may play some part in the production of ketosis in ruminants given diets high in protein. Clearly, however, the carbon-containing moiety cannot be used directly for direct re-synthesis of the corresponding amino acid by amination or transamination.

Ammonia arises not solely from de-amination of amino acids and urea. Nitrogenous bases such as choline and betaine give rise to ammonia. Nitrates and nitrites are reduced to ammonia (Lewis, 1951) and desamidases in the rumen liquor produce ammonia from amines such as asparagine and glutamine. Ammonia is thus a common metabolite in the complex events of protein metabolism in the rumen, but the rate at which it is produced varies considerably with the food substrate involved.

Not all the ammonia which is produced in the rumen is absorbed into the portal blood. At the same time that de-amination of dietary protein is taking place net synthesis of protein occurs (PEARSON and SMITH, 1943), and this increase in synthesis is associated with a marked increase in the numbers of the free living iodophilic cocci of the rumen and disappearance of ammonia (SMITH and BAKER, 1944). The major factor which determines the rate of synthesis appears to be the ratio of nitrogen to energy yielding constituents. Ample carbohydrate other than cellulose must be present if the large quantity of ammonia is to be " trapped " by a rapidly proliferating flora. Protein utilization and energy utilization in the rumen are therefore very closely linked. Thus one finds that the fermentation of the cellulose of a ration free of nitrogen is incomplete since the salivary urea does not supply sufficient ammonia for bacterial proliferation. Similarly protein formation is incomplete when rations high in soluble protein—or non-protein nitrogenous constituents—are given because there is not a sufficient source of energy for the growth of the bacterial population.

The *in vitro* studies give little indication of the rate of synthesis or of de-amination of protein under natural conditions, and certainly none concerning the quantity of microbial protein which passes to the abomasum and which is subsequently digested. It is now known that earlier extreme views that the ruminant lives entirely on a diet of microbial protein are incorrect. By feeding sheep, zein, an alcohol soluble protein containing no lysine, MCDONALD (1948b) was able to show from estimates of the lysine and alcohol soluble protein leaving the stomach that only about 40 per cent of the zein of the diet was converted in the rumen to microbiological protein. Since the iodophilic cocci characteristic of the rumen are absent from the faeces it may be assumed that their digestion is fairly complete and that the sheep obtains 40 per cent of its protein supply from the microbial protein and 60 per cent from its food protein. Similar results using a different approach have been obtained in Australia (MOIR and WILLIAMS, 1950). The protein which is synthesized in the rumen, which consists in the main of the bodies of iodophilic cocci, has been examined in some detail. The bacteria have been isolated, and shown to contain some 40 per cent of a starch-like polysaccharide and about 7 per cent of mineral matter. When this dried bacterial preparation from cattle was fed to rats it was found that its biological value was 88 and its true digestibility 73 per cent (MCNAUGHT *et al*, 1950). In similar studies in Australia, the biological value of bacterial protein from sheep was found to be 80 and the true digestibility 65 per cent (REED *et al*, 1949). These figures may be compared with those obtained for more usual foods. Thus milk protein has a biological value of 93 and a true digestibility approaching 100. Rumen bacteria have a high biological value, implying an adequate amino acid balance, but a low digestibility. In actual fact they approximate fairly closely to yeast protein which has a biological value in rats of 85 and a true digestibility of 74.

These results suggest that the rumen protein has a relatively high nutritive value to the host animal. Further evidence of its value comes from the fact that the protein isolated from the rumen of sheep given rations almost devoid of amino acids contains all the so-called 10 essential amino acids (LOOSLI *et al*, 1949). Furthermore, the urine and faeces of the sheep in these experiments contained appreciable quantities also. There is, however, some evidence that microbial protein is low in sulphur-containing amino acids, notably in methionine. It is probable that some of the differences between the sheep and cow in the biological value of comparable dietary proteins (*see* Table 1.9) is due to the greater need for sulphur-containing amino acids on the part of sheep. Wool contains 13·6 per cent of cystine and 0·7 per cent of methionine, milk proteins 1·0 per cent and 3·2 per cent respectively, and muscle proteins 1·2 per cent cystine and 3·2 per cent methionine. The mixed proteins of the rumen contents of sheep existing almost entirely on urea (Loosli *et al*, 1949) contain less than 1·0 per cent methionine, in fact rumen bacteria are mildly deficient in methionine (Reed *et al*, 1949). It is not surprising, therefore, to find that the addition of methionine to diets containing urea as the major source of nitrogen, results in an increase in nitrogen retention and growth (LOFGREEN *et al*, 1947). On similar types of ration the addition of sulphate also increases the retention of dietary nitrogen, suggesting that the metabolism of sulphate in the rumen leads to the formation of sulphur-containing amino acids.

The lack of variation in the biological value of different dietary proteins in ruminants is remarkable and appears to be contingent upon the fermentations involving nitrogen-containing constituents in the rumen. First, not all the ammonia produced may be trapped by proliferating bacterial cells, and secondly, the proteins of these bacteria contain a fairly constant proportion of those amino acids known to be essential for the host. Possibly bacterial synthesis of methionine is a major factor determining the nutritive value of the nitrogen-containing moieties of the ruminant's diet, but unfortunately exact estimates of the rate of synthesis of specific amino acids is not known. Amino-acid synthesis needs to be immense to support lactation in the cow, since secretion of milk proteins can more than quadruple the amounts of amino acids required for her mere subsistence.

The biological value of dietary protein is only one factor to be considered in estimating the requirements of ruminants for a dietary source of nitrogenous constituents. Faecal losses, which are specifically discounted in estimating the biological values of proteins, are particularly large in ruminants. Table 1.10 gives typical results for the quantitative analysis of the food and excreta of a sheep subsisting on hay and maize and a suckling calf subsisting on milk. Both were given similar quantities of dietary nitrogen. It will be noted that the loss of nitrogen in the faeces of the sheep is very considerably greater than that in the faeces of the calf. This faecal nitrogen, however, is not simply that present in the proteins, nucleic acids and other constituents of the feed which have resisted bacterial action in the rumen, true enzymatic digestion in the gut and further bacterial degradation in the caecum.

TABLE 1.10

NITROGEN METABOLISM OF A SUCKLING CALF AND A GROWING, RUMINATING LAMB

Species	N *intake*	*Loss in faeces*	*Loss in urine*	*Body storage*
Suckling calf*	14·96	0·88	13·54	0·54
Growing lamb	12·67	5·36	3·54	3·73

* At nearly treble this level of feeding the calf stored 25·0 g. nitrogen daily (Blaxter and Wood, 1952b).

Conventionally faecal nitrogen may be regarded as consisting of two parts. The first portion, the metabolic faecal nitrogen, represents the residues of unabsorbed digestive juices and the cellular detritus abraded from the mucosa of the gut during the passage of the fibrous feed residues. It tends to be independent of the nitrogen of the feed. The second is a smaller fraction which is proportional to the amount of protein ingested and hence can be legitimately classed as a feed residue. The metabolic faecal nitrogen in ruminants, usually defined and measured as the nitrogen excreted in the faeces when the diet contains no nitrogen, amounts to about 0·5 g. nitrogen/100 g. dry matter ingested. This value of 0·5 g. is considerably higher than comparable values obtained for simple-stomached animals such as man and rats, where a more usual estimate is 0·2 g. nitrogen/100 g. dry matter ingested This high " basal loss " of nitrogen in the faeces involves a continuous drain on the protein economy of the animal (BLAXTER and MITCHELL, 1948; LOFGREEN, LOOSLI and MAYNARD, 1951) and it may be shown that the need to replace this loss of tissue and secretions represents one of the major portions of the requirement of ruminants for protein. Some feeds, low in protein and high in fibre, do in fact result in a greater loss of nitrogen in the faeces of the ruminant than they in fact supply to the animal in the first place. Since the faecal metabolic nitrogen is so high in ruminants, it follows that the true digestibility of most feeding-stuffs by ruminants is higher than the usually quoted values might suggest and are comparable in fact to values obtained with animals with simple stomachs. That this is so has been demonstrated by techniques in which it was found that the nitrogen content of isolated feed residues in the excreta is particularly small (MUKHERJEE, 1946).

The reason for the large loss of metabolic nitrogen in the faeces, or rather the reason for the partial failure for reabsorption of digestive juices to take place, as it undoubtedly does in other species, is probably associated with the large mass of fibrous food residues in the intestine. Contributory factors are probably bacterial proliferation in the lower gut, since bacterial activity there would " trap " simple nitrogenous compounds with no possibility of subsequent digestion of the microbial protein such as takes place following similar types of reaction in the rumen.

FAT SOLUBLE VITAMINS

From the foregoing discussion it is evident that the ruminant animal is to a large extent independent of its diet for a source of many of the essential amino acids it requires and for all the B complex vitamins, always provided that a substrate in the rumen is provided which allows for their synthesis. This independence does not apply to the fat soluble vitamins with the sole exception of vitamin K, which is synthesized by the microflora of the gut by most species, ruminants included.

That vitamin A is a dietary essential for cattle in the form of carotene has been known for a very long time, and in certain areas of the world deficiencies have assumed enzootic proportions. β carotene from grass and other products is absorbed to the extent of 30–40% from the digestive tract of the cow (SESHAN and SEN, 1942). In the intestinal wall it is converted into vitamin A which is transported to the liver largely by means of the intestinal lymph (THOMPSON, GANGULY and KON, 1947). Contrary to early supposition, β carotene is not converted into vitamin A in the liver. A number of deficiency syndromes have been observed in cattle due to lack of β carotene or vitamin A in the ration. In young calves deficient in vitamin A, intracranial pressure increases due to the fact that bone growth is suppressed, whereas the growth of the nervous system proceeds unchecked (MOORE, 1939; MOORE and SYKES, 1941). Optic stenosis follows and permanent blindness results. A full account of the pathological changes to be found in young dairy animals subjected to experimental hypovitaminosis A has been given by HELMBOLDT *et al* (1953). Such effects can be elicited by rations which are composed of sugar-beet pulp and many grains, if no hay of good quality is provided. In bulls, deprivation of vitamin A leads to impotence and degeneration of the seminiferous tubules of the testis (ERB *et al*, 1944). In heavily fed cattle, generalized oedema or anasarca occurs (MADSEN and EARLE, 1946). The importance of the latter condition may be judged by the fact that 590 carcasses were condemned for this fault in a period of 5 years in the U.S.A. (MADSEN *et al*, 1948). In pregnant animals the effect of deficiency is generally seen in the birth of a weak or blind calf which usually succumbs. It is only in range cattle that the classical xerophthalmia of vitamin A deficiency is seen.

Vitamin D deficiency is of relatively rare occurrence in cattle, though it can be produced with difficulty under experimental conditions. Normally cattle receive sufficient vitamin D activity from sun and skyshine, and so do sheep, but, nevertheless rickets-like conditions which respond to vitamin D therapy do occur in both species. Many years ago ELLIOT and CRICHTON (1925) described " bent leg ", a naturally occurring condition in sheep simulating rickets, which could be prevented either by giving vitamin D in the form of small doses of cod-liver oil, or by increasing the calcium content of the diet. This fact demonstrates that rickets is not synonymous with vitamin D deficiency ; in fact, with many laboratory species it is impossible to demonstrate a need for vitamin D unless the calcium/phosphorus ratio is abnormal or there is a relative deficiency of one or other element. Some rachitic calves respond to vitamin D just as do sheep with " bent leg ", but this does not necessarily mean their ration is deficient in vitamin D or that they fail to get sufficient sunshine. Many of the cases of rickets in young cattle are due to mineral shortage rather than vitamin D deficiency.

A rickets-like disease occurs in both New Zealand and England in sheep which graze on various fodder crops, notably oats during the winter months (EWER, 1949). Such crops, judged from chemical analyses, provide highly adequate amounts of calcium and phosphorus, the calcium/phosphorus ratio is normal, and the sheep are kept outside, thus presumably receiving winter sunshine and skyshine. That the disease is indeed rickets may be judged by the fall in the phosphate content of the blood, and by the changes noted in the metacarpal epiphyses and the costochondral junction at death. These are exactly comparable to those noted in true rickets. Furthermore, the leg weakness can be prevented by massive dosages of calciferol. In this respect, however, although estimates of the requirement of the sheep for vitamin D are 130 i.u. daily (ANDREWS and CUNNINGHAM, 1946) supplements of 300 i.u. vitamin D have not been sufficient to prevent the disease in young sheep grazing green oats. Clearly some factor interfering in phosphorus metabolism is involved and its nature at present is unknown.

Interest in vitamin D, calcium and phosphorus in relation to ruminant nutrition has further increased during recent years as the result of suggestions that infertility in cows arises as a result of either inbalance of the ration with respect to the calcium/phosphorus ratio, low phosphorus intakes being associated with infertility, or, alternatively, an insufficiency of the vitamin D supply (HIGNETT and HIGNETT, 1953; ABRAMS, 1952). At the present time, however, no information is available regarding the primary reproductive defect responsible for the infertility of the animals concerned, and until more information is obtained no definite and unequivocal conclusions regarding the role of vitamin D in reproductive performance is possible.

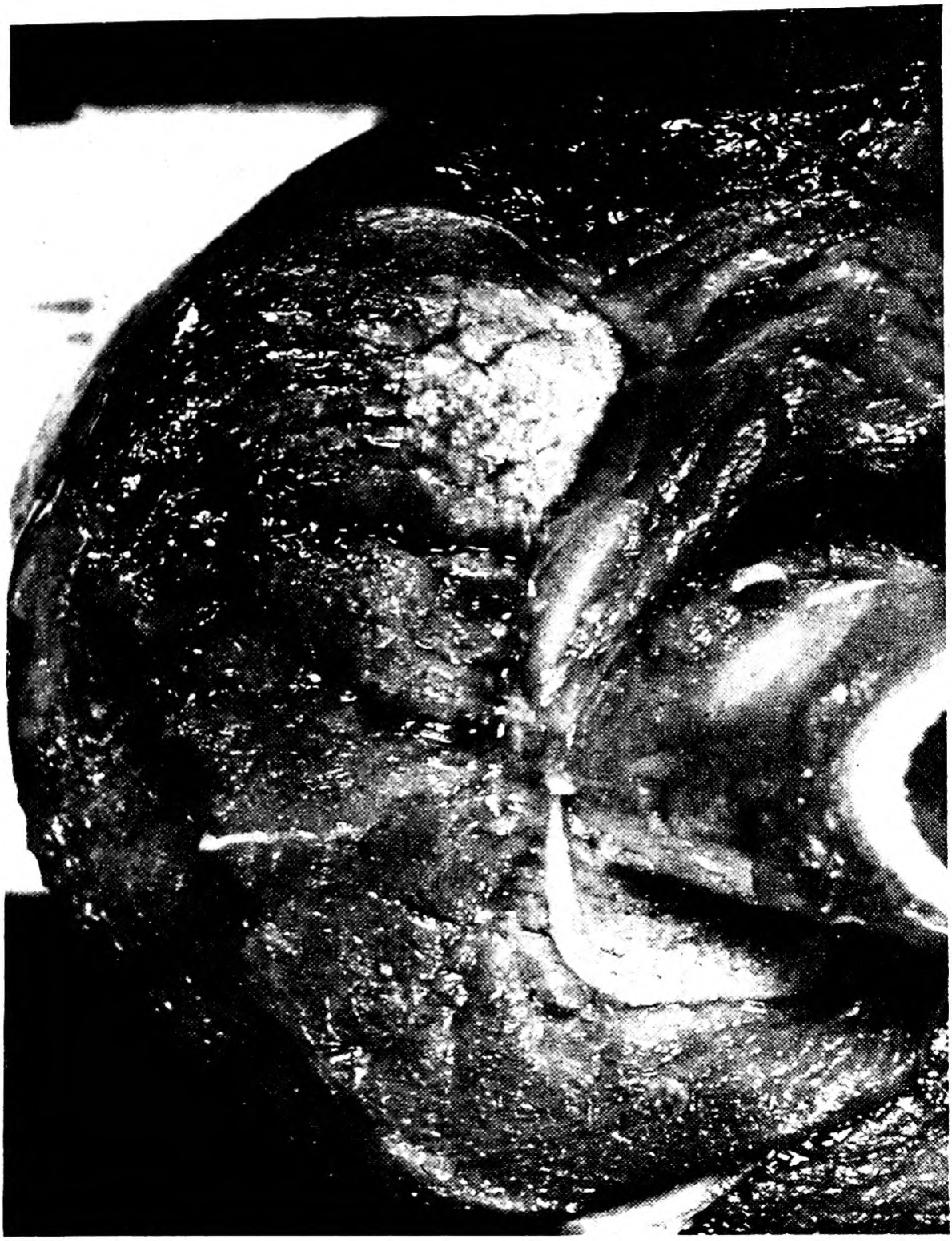


Figure 1.6. A cross-section through the femur of a calf suffering from muscular dystrophy. The white areas of degenerating muscle can be seen surrounded by muscle which still remains normal.

The early enthusiasm for the use of vitamin E in the treatment of sterility in cattle was not confirmed by either practical results or experimental observations. Vitamin E, however, is intimately concerned in the nutrition of both sheep and cattle since it will prevent and cure certain types of muscle degeneration which occur under natural conditions (WILLMAN *et al*, 1945; BLAXTER and SHARMAN, 1953). This degenerative disease is characterized by white discoloration of the muscles as shown in *Figure 1.6*, while histological examination reveals that the primary change is a loss of the proteins of the muscle cell. The disease has been produced experimentally in both cattle (BLAXTER, WATTS and WOOD, 1951, 1952) and sheep (CULIK *et al*, 1951) by feeding rations containing but very small amounts of vitamin E. These rations have all contained lard, and further work has shown that the inclusion of unsaturated fat in the experimental diet leads inevitably to a considerable exacerbation of clinical signs and a marked increase in the muscular degeneration found on slaughter. Cod-liver oil, or more specifically the unsaturated fatty acids it contains, is particularly active in this respect, and its addition to diets otherwise quite adequate can produce muscular dystrophy. Addition of vitamin E reverses this effect. In Britain it appears from recent studies that muscular disease, preventable and curable by vitamin E therapy, is very widespread. In certain areas of the north of Scotland where beef cows are wintered on very poor rations of turnips and straw, the incidence in the suckling calves has been as high as 95 per cent, while tentative estimates suggest an average incidence of muscular dystrophy in herds rearing beef cattle of 20–25 per cent (BLAXTER and BROWN, 1952–3).

It is thus clear that the ruminant mode of nutrition does not confer any advantages to the host animal as far as protection against the effects of dietary deficiencies of the fat soluble vitamins are concerned. Vitamin A deficiency reaches enzootic proportions in many areas of the world and so indeed do disease entities prevented by vitamin E. Though our evidence is as yet incomplete, even with vitamin D there is an indication that areas exist where its administration is necessary if ruminants are to thrive.

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CHAPTER 2

PIG NUTRITION

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THE LIFE of a pig begins with the fertilization of the ovum. Details concerning embryonic growth and factors affecting it are, as yet, lacking. Some recent information on the development of pigs' embryos is given in Table 2.1 (*see also Figure 2.1*). The weight of a pig at birth, which is, to some extent, a measure of the conditions governing embryonic development, is also a guide to the animal's post-natal growth potential. Table 2.2 gives some data pointing to the existence of a definite relationship between birth weights and weaning weights. Generally, the heavier a pig is at birth the faster is its rate of growth.

TABLE 2.1

EMBRYONIC DEVELOPMENT OF A PIG (according to *Nutrition News Bulletin*, 1951)

Age of the embryo days	*Length inches*	*Weight oz.*
30	1	0·06
60	4·5	3·3
80	8	11·75
90	8·7	24·0
106	9·5	40·0
114	11·0	49·0

A pig is born fairly mature physiologically. At birth it is covered with a hair-coat, it has sharp teeth, it can see, it can walk, and immediately after birth it will instinctively find its mother's udder and start to suckle and so obtain nourishment.

It has been established that a pig, like a calf, and unlike a human baby, depends on colostral transfer of immunity. The anatomical structure of the placenta points to a post-natal transfer. In the pig, the maternal and foetal circulations are separated by several tissue layers which block the transfer of antibodies, whereas in man antibodies traverse easily the placental barrier as there is but one tissue layer. YOUNG and UNDERDAHL (1950) found no trace of neutralizing antibodies in the serum of new born pigs from sows immunized against influenza before pregnancy. However, the colostrum of the sows had high titres of both neutralizing and haemaglutination inhibiting antibodies which were passed to the young in relatively high titres within 24 hours after nursing started.

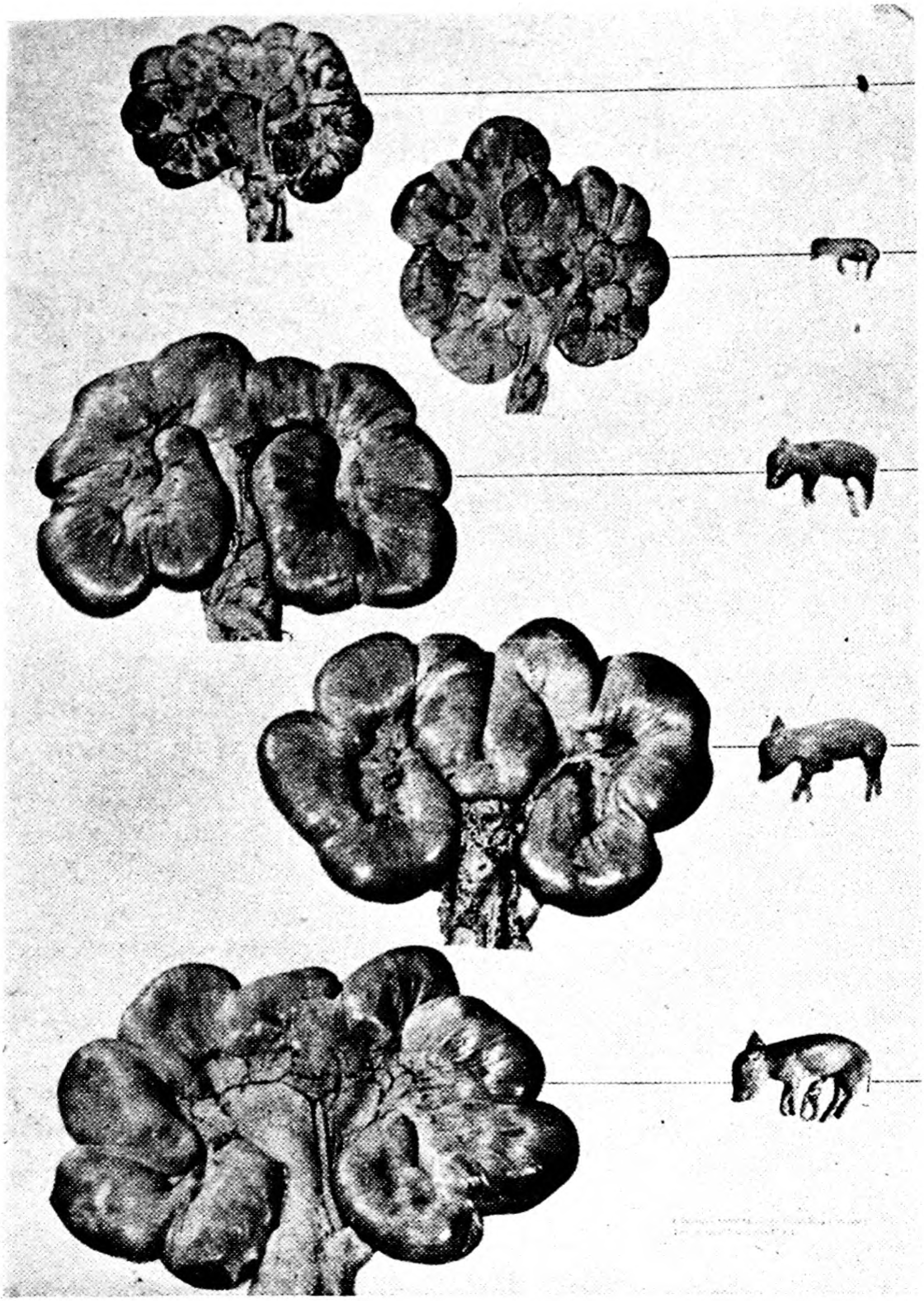


Figure 2.1. Size of the uterus and foetus at different stages of pregnancy (30, 60, 80, 90 and 110 days). (By courtesy of the Ralston Purina Company, St. Louis, Missouri and the Meredith Publishing Company, Des Moines.)

At birth, the euglobulin fraction in the blood is nil, but it increases rapidly after ingestion of colostrum. It becomes low again after 3–4 weeks and rises to reach the normal value, 65 mg./100 ml. blood, in 5 or 6 months.

TABLE 2.2

RELATIONSHIP BETWEEN BIRTH WEIGHT AND WEANING WEIGHT

(based on 900 piglets from one herd)

Birth weight *lb.*	*Weaning weight* *lb.*
1·6–1·8	22·4
1·9–2·1	26·1
2·2–2·4	28·0
2·5–2·7	28·8
2·8–3·0	29·3
3·1–3·3	33·5
3·4–3·5	33·4

At birth, the serum protein concentration in pigs is less than one third that of the sow. It increases rapidly during the first few days of life but does not reach the value for mature pigs till about 6 months later (mature value approximately 1,100 mg./100 ml. of blood).

Electrophoretic studies of the blood plasma of the sow during gestation and parturition, and of the new born and young pig point to a gradual decline in the gamma globulin component of the blood of the sow throughout the gestation period, to a sharper decline during the first 24 hours post-partum, and to a very marked increase in this component of the blood in the first 24 hours of a piglet's life. For example, at birth the concentration of gamma globulin may be as low as 1·3 mg./ml., and after the first 24 hours it may increase to 20·3 mg./ml. (FOSTER *et al*, 1951). It appears that the gamma globulin is mobilized by the sow during gestation, stored in the udder and released to the new born through the colostrum. Thus, the importance of colostrum as a medium for transfer of antibodies has been demonstrated, and the inability, under normal conditions, to raise piglets deprived of colostrum explained. It is interesting to note that recently pigs have been reared without colostrum after being caught at birth into a sterile canvas bag and placed in an isolated environment (YOUNG and UNDERDAHL, 1951). The critical factor appears to be a strict isolation affording protection against infection.

SOW'S COLOSTRUM AND MILK

THE EJECTION OF MILK

The natural food for new born pigs is sow's colostrum and milk, and their quality and quantity have received much attention during recent years. The interest arose after a new method for obtaining satisfactory samples was introduced by Braude and his associates (1947). Until then it was very difficult, if not impossible, to obtain satisfactory samples of sow's milk. A sow controls her let-down of milk so effectively that milk cannot be obtained from her by milking in the way usually effective with other large animals. Samples obtainable in the past, only by subterfuge during natural suckling, were very small, from one or two teats only, and generally unsatisfactory. Following Ely and Petersen's (1941) suggestion that the posterior pituitary hormone, oxytocin, is responsible for the let-down or ejection phenomenon, Braude *et al* (1947) obtained milk samples from the sow after an intravenous injection of the hormone. This procedure is now used whenever samples of sow's milk are required. Whittlestone (1952) recently demonstrated that the vasopressor (anti-diuretic) hormone of the posterior pituitary also causes a let-down of milk in the sow.

Braude and Mitchell (1950) studied the dose response to oxytocin in the sow, and Table 2.3 summarizes their findings. It is obvious that there is a definite relationship between the dose of the hormone injected, the amount of milk and the duration of milking. It takes only 10–20 seconds from the time of injection of the hormone to the commencement of the milk flow. The duration of effectiveness of the hormone depends on the time it is present in the blood stream, but the factors controlling its presence are, as yet, unknown. It is also not known what mechanism is involved in releasing the hormone at regular intervals by the pituitary glands during natural lactation, nor what its actual mode of action is. The most likely hypothesis is that

TABLE 2.3

EJECTION OF MILK IN THE SOW

Dose response to Oxytocin given as Pitocin (Parke, Davies and Co.)
(according to Braude and Mitchell, 1950 and unpublished data)

Dose of hormone i.u.	*Yield of milk ml.*	*Time between end of injection and milking sec.*	*Duration of milk flow sec.*	*Dose of hormone i.u.*	*Yield of milk ml.*	*Time between end of injection and milking sec.*	*Duration of milk flow sec.*
1/96	0·6	20·0	13·8	3	78·0	11·2	131·0
1/64	1·4	20·9	19·6	5	82·0	11·4	182·0
1/48	4·8	20·5	14·8	7½	85·9	11·6	239·0
1/32	10·2	17·7	33·3	10	105·0	10·8	259·0
1/16	10·3	15·1	19·7	11¼	128·5	11·4	253·0
⅛	11·1	14·1	21·7	12½	125·0	11·6	378·0
¼	19·0	13·9	33·9	15	142·5	11·4	284·0
½	45·0	12·9	63·7	17½	142·2	10·1	295·0
1	48·0	12·4	85·2	20	128·0	10·2	234·0

the hormone causes the myo-epithelial cells surrounding the alveoli in the mammary gland to contract (RICHARDSON, 1949) which, in turn, results in the expulsion of milk.

The reaction of the sow to the injection of oxytocin appears to be so regular that Whittlestone (1952) suggested that the sow should be used as an assay animal for the milk ejecting activity of different preparations.

It is interesting that during parturition the pituitary releases oxytocin to assist with the contraction of the uterus. The presence of the hormone in the blood stream is responsible for the fact that during farrowing the colostrum can be collected without difficulty by milking the sow without administration of the hormone.

As described later, at each natural suckling the piglets obtain 25–35 g. of milk, an amount equivalent to that obtained when inducing let-down artificially with $\frac{1}{4}$–1 unit of oxytocin. In conjunction with the evidence presented in Table 2.3, it appears that the amount of milk piglets receive at each suckling is limited by the amount of the hormone released by the pituitary.

THE QUALITY OF MILK

In Table 2.4 the chemical composition of sow's colostrum and milk is given as obtained by the Shinfield workers (Braude *et al*, 1947 and

TABLE 2.4

THE CONSTITUENTS OF SOWS' COLOSTRUM AND MILK
(according to Braude *et al*, 1947, and unpublished data)

		Colostrum	*Milk*
Total solids	g./100 g.	25·76	19·89
Fat	g./100 g.	4·43	8·25
Solids not fat	g./100 g.	21·33	11·64
Protein	g./100 g.	17·77	5·79
Lactose	g./100 g.	3·46	4·81
Ash	g./100 g.	0·63	0·94
Calcium	g./100 g.	0·053	0·25
Phosphorus	g./100 g.	0·082	0·166
Vitamin A	i.u./g. fat	71·1	11·0
Vitamin D	i.u./g. fat	—	0·55
Vitamin C	mg./100 ml.	30·06	13·0
Thiamine	μg./100 ml.	96·8	67·7
Riboflavin	μg./100 ml.	135·0	137·0
Nicotinic acid	μg./100 ml.	165·0	836·0
Pantothenic acid	μg./100 ml.	130·0	427·0
Pyridoxin	μg./100 ml.	2·5	20·0
Biotin	μg./100 ml.	5·3	1·4
Vitamin B_{12}	μg./100 ml.	0·15	0·17
Iron*	μg./100 g.	265·0	179·0
Copper†	μg./100 ml.	—	20–134

* According to Venn, McCance and Widdowson (1947). † According to Carpenter (1947).

unpublished data). Recently a number of other reports on the subject has appeared, showing a substantial measure of agreement. Braude *et al* (1947) and SMITH (1952a, 1952b), studied lactational trends of the major constituents of sow's milk. BEACOM and BOWLAND (1951) produced figures for the amino acid composition of sow's colostrum and milk, and these appear in Table 2.5. A more detailed study of the different components of the milk was undertaken by the Wisconsin workers (SHEFFY *et al*, 1952a, 1952b), and recently they published data on the nitrogen constituents and on the fat and phospholipid content of sow's milk. The protein content of the milk was 6·4%, and the nitrogen in it was distributed in the following way: casein 57–58%, albumin 7–8%, globulin 10%, proteoses-peptons 17–18% and non-protein nitrogen 7–8%. It is interesting to note that the amount of casein in the colostrum was only about 40 per cent of the total protein, and that, while the total protein decreased markedly from colostrum to milk, the non-protein nitrogen increased markedly, and continued to increase with advancing lactation. The differences in the composition of the sow's diet had no effect on the protein of their milk. The authors compared the effect of a maize-soyabean ration with and without tankage or vitamin B_{12}, and found no appreciable differences in the composition of the milk. Apparently, the organic and inorganic constituents of milk, with the exception of fat, vitamins and trace elements, remain relatively constant under wide variation of diet.

TABLE 2.5

AMINO-ACID COMPOSITION OF THE COLOSTRUM AND MILK OF THE SOW (AS PERCENTAGE OF PROTEIN)
(according to Beacom and Bowland, 1951)

	Colostrum	*Milk*
Arginine	6·0	5·7
Histidine	2·1	2·2
Isoleucine	3·9	4·2
Leucine	9·1	8·0
Lysine	6·5	7·4
Methionine	1·2	1·4
Phenylalanine	4·1	3·5
Threonine	5·2	3·5
Valine	6·3	5·0

The composition of sow's milk fat, as indicated by the fat content, closely resembles that of the depot fat in pigs, and that of lard, suggesting that the mammary gland of the pig exerts little or no effect on the depot fats as they are being utilized in the elaboration of milk fat. Thus, the level of feeding (caloric intake), during gestation and lactation may, by affecting the degree of fatness of the animal, affect the content of fat in milk.

The sow's milk fat contained 1·39–1·77 per cent of phospholipids. The iodine value varied from 66·3 to 68·9. The saponification number from 185·2 to 192·6, and the Hahner value from 91·1 to 92·6. In colostrum the phospholipid content, the saponification number and the Hahner value were about the same as in milk, whilst the iodine value was markedly higher, 80·5–81·9.

The specific gravity of sow's milk was 1·038, its *p*H 6·99 and its freezing point −0·563°C.

THE QUANTITY OF SOW'S MILK

A number of studies were undertaken on the milk yield of the sow. The way to obtain information on the quantity of milk produced by a sow is by weighing her litter before and after suckling—the difference in weight indicating the quantity of milk received by the piglets. An alternative to achieve the same aim would be to weigh the sow immediately before and after suckling, but this form, though practised in Denmark, requires a specialized weighing equipment, and deals with the litter as a whole and not with individual piglets.

Smith (1952a) and **Barber**, **Braude** and **Mitchell** (unpublished) have made some observations on the suckling procedure as a preliminary step to their studies on lactation in the sow. They have established that regardless of age, normal piglets suckle at approximately one-hour intervals throughout the day and night. This finding is of considerable consequence when interpreting the data on milk yield in sows, found in the literature (see Table 2.6). Most of these data were based on estimations carried out at longer intervals between sucklings, 2–6 hours, and **Barber** *et al* (unpublished) showed conclusively that such an unnatural procedure resulted in a gross underestimation of the true milk yield. They weighed the piglets before and after suckling, at 1-hour intervals between sucklings throughout a 48-hour period during each week of lactation. The piglets were separated from their dams, and every hour were let into the pen for suckling. Invariably, as soon as they appeared in the pen the sow lay down and within a few minutes allowed them to suckle. Some data on the suckling performance are recorded in Table 2.7. It is known that the suckling consists of two distinct phases: at first, piglets vigorously nose the sow's udder, and then, suddenly, they all quieten down, draw back their ears and appear to take in the milk. Actually, we have observed that the second period is divided into two. During the first half, the pigs, although quiet, do not get any measureable quantity of milk, while only during the second half is the milk ejected. At present there is no physiological explanation of this suckling behaviour. The time during which the milk actually flows is very short,

Table 2.6

SUMMARY OF THE ESTIMATION OF MILK YIELD IN SOWS MADE BY VARIOUS WORKERS AND THE METHODS EMPLOYED TO OBTAIN SUCH ESTIMATIONS

Breed	*Interval allowed between controlled sucklings (hr.)*	*Average daily milk yield (lb.)*	*Authors*
Yorkshire	3	2·75	Gohren (1865)
Poland China and Chester White	2 by day 4–5 by night	5·20	Henry and Woll (1897)
Berkshire	2 by day 4 by night	6·31	Carlyle (1903)
Poland China		4·86	
Razorback		5·17	
Berkshire	2 by day 3 by night	5·56	Davies (1904)
Duroc Jersey and Berkshire	Not given	5·81	Smith (1921)
Landschwein	3	6·90	Schmidt and Lauprecht (1926)
Landschwein	3	7·35	Hempel (1928)
Landschwein	3	5·92	Ohligmacher (1928)
Landschwein	3	4·05	Rodewald (1928)
Mangalicza	Not given	5·02	Racz (1931)
Russian Landrace	—	7·47	Borowsky and Kwasnitsky (1932) (quoted by Niwa *et al* (1951))
Edelschwein	2–3	7·17	Schneider (1934)
Not given	2–6	7·70	Hughes and Hart (1935)
Large Black (*a*) Gilts and sows	2–3	6·55	Bonsma and Oosthuizen (1935)
(*b*) Gilts		6·04	
Mangalicza	2	6·42	Contescu, Roman and Breaban (1937)
Large White		7·14	
Landschwein	—	11·40	Ostertag and Zuntz (1908)
Landschwein	Approx. 1½	10·52	Wohlbier (1928)
Edelschwein	Approx. 1½*	8·02	Albig (1940)
Yorkshire	Approx. 1–2	10·41	Olofsson and Larsson (1930)
Poland China and Duroc Jersey	Some 1 Some 2	11·70	Wells, Beeson and Brady (1940)
Middle White	Approx. 1	9·33	Niwa, Ito, Yokoyama and Otsuka (1951)
Berkshire (*a*) Gilts and sows	1–1¼	14·40	Smith (1952a)
(*b*) Gilts		10·73	
Berkshire	1–1¼	12·07	Smith (1952b)
Large White—gilts	1	13·71	Barber, Braude and Mitchell (unpubl.)

* With an interval of 4 hr. between 12 midnight and 4.0 a.m.

about 20 seconds at each suckling. In natural suckling this is followed by nosing of the udder, similar to that which takes place before the milk ejection.

Table 2.7

SUCKLING PERFORMANCE OF PIGS

(according to Barber, Braude and Mitchell, unpublished data)

	Sow No. 1	*Sow No. 2*	*Sow No. 3*
No. of pigs born and reared	11	11	10
Time taken by the sow to lie down after the pigs entered the pen, sec.	12	17	11
Nosing, sec. : Mean	96	76	85
Range	56–140	55–100	60–120
Quiet period, sec.	23	16	21
Suckling, sec.	19	20	17

In Table 2.8 the lactation milk yield of three sows is recorded together with some data concerning the milk intake of individual pigs, and in *Figure 2.2* typical lactation curves are plotted. In the material collected at Shinfield there was considerable variation in the milk yield of different sows. Smith (1952a) working in New Zealand obtained rather similar results.

Table 2.8

MILK YIELD OF SOWS

(according to Barber, Braude and Mitchell, unpublished data)

	Sow No. 1	*Sow No. 2*	*Sow No. 3*
No. of pigs born and reared	11	11	10
Total lactation yield, kg.	401·4	348·2	295·0
Mean milk intake per pig per lactation, kg.	36·5	31·7	29·5
Mean milk intake per pig per day, g.	676	587	546
Mean intake per pig at each suckling, g.	28·2	24·4	22·8

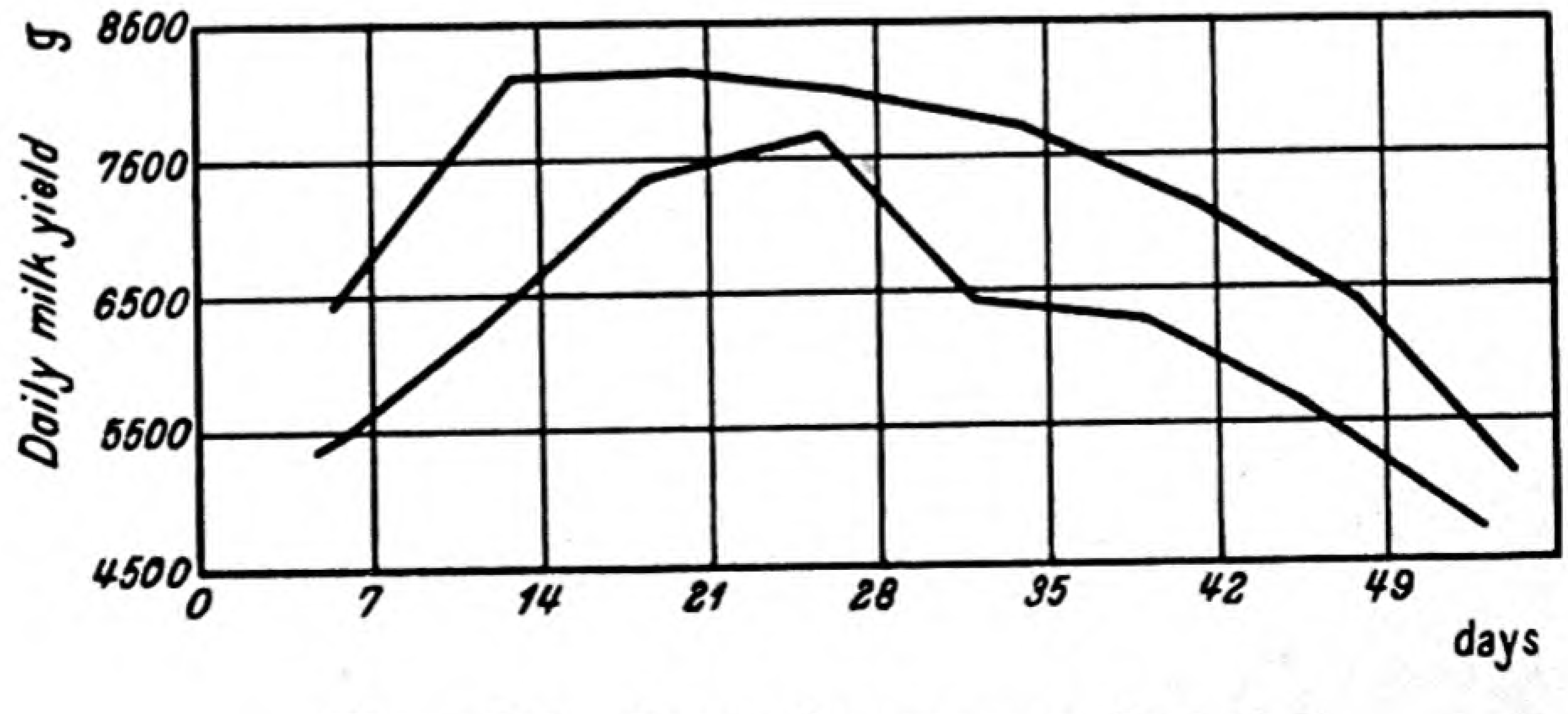


Figure 2.2. Lactation curves of sows.

Quite considerable differences in the milk yield from different teats of the same sow were observed. Each gland is known to be an independent and complete unit. Data in Table 2.9 illustrate, for example, that anterior teats usually produce more milk than the other teats. Smith (1952a) indicated that there are significant differences in the quality of the milk from different teats. However, both these statements are based on rather limited data.

TABLE 2.9

INTAKE OF MILK BY PIGS SUCKLING THE ANTERIOR TEATS OF SOWS COMPARED WITH THE MEAN FOR THE WHOLE LITTER
(according to Barber, Braude and Mitchell, unpublished data)

		Sow No. 1	*Sow No. 2*	*Sow No. 3*
Milk intake per pig per lactation, kg.	mean	36·5	31·7	29·5
	left fore	40·4	42·9	25·6
	right fore	45·7	42·5	36·0
Milk intake per pig per day, g.	mean	676	587	546
	left fore	748	794	474
	right fore	846	787	666
Milk intake at each suckling, g.	mean	28·2	24·4	22·8
	left fore	31·2	33·1	19·8
	right fore	35·3	32·8	27·8
Milk consumed per g. live weight gain in 21 days, g.	mean	3·96	3·93	4·12
	left fore	3·88	3·98	4·27
	right fore	4·02	3·77	4·58

MILK SUBSTITUTES AND ARTIFICIAL REARING OF PIGS

The increasing knowledge of the composition and yield of sow's milk led to attempts to produce a suitable replacement for it. Cow's milk is not a satisfactory substitute for sow's milk. Reasonable rearing results, however, were obtained with cow's milk fortified with 60 g. sucrose, 2·5 g. ferrous sulphate, 0·2 g. cupric sulphate, 0·2 g. manganous sulphate, and 0·02 g. potassium iodide per litre (Anderson and Hogan, 1950a). One of the first to succeed in producing a milk substitute was Johnson and his co-workers (1948); they were followed by many others. Table 2.10 gives values, based on Shinfield analytical data, on a calculated intake of nutrients by a piglet consuming 850 g. of sow's milk daily. These are compared with the amount of nutrients a piglet would receive from a milk substitute prepared according to

TABLE 2.10

DAILY CONSUMPTION OF NUTRIENTS BY YOUNG PIGS*

	A pig consuming daily 850 g. of milk would receive :				
	When suckling	*When fed substitute as used by Johnson et al* (1948)		*When suckling*	*When fed substitute as used by Johnson et al* (1948)
Total solids	169 g.	170 g.	Vitamin C	111 mg.	—
Fat	71 g.	45 g.	Thiamine	575 μg.	552 μg.
Protein	49 g.	51 g.	Riboflavin	1165 μg.	1105 μg.
Lactose	41 g.	64 g.	Nicotinic acid	7106 μg.	2210 μg.
Ash	8 g.	10 g.	Pantothenic acid	3630 μg.	6630 μg.
Ca	2·1 g.	1·7 g.	Pyridoxin	170 μg.	552 μg.
P	1·4 g.	1·2 g.	Biotin	12 μg.	8·5 μg.
Vitamin A	770 i.u.	850 i.u.	Vitamin B_{12}	1·4 μg.	—
Vitamin D	39 i.u.	85 i.u.			

* Using data from Table 2.4 concerning the composition of sow's milk.

Johnson's recommendations. In most instances there is a good measure of agreement between the two sets of values.

Table 2.11 gives the composition of a typical milk substitute. Obviously this is based on the available knowledge of the composition of sow's milk, but many details are quite empirical. When preparing milk substitutes, there is a general tendency to allow a wide margin of safety in the amounts of individual nutrients. The success with the laboratory formulas has led to the development of commercial substitutes for sow's milk, and thence to artificial rearing of pigs.

The method of artificial rearing consists of leaving the piglets on the sow for 48 hours or more after parturition, during which time they have access to the sow's colostrum, and rearing them thereafter on a milk substitute. The method is still in its infancy, but has great possibilities. Compared with the orthodox method of rearing pigs on a sow, the following advantages are claimed for the artificial rearing.

1. *More pigs reared per litter through reduction in losses and saving of surplus pigs.* The heavy losses of pigs, amounting on an average to 25–30 per cent of the pigs born alive, could be reduced substantially by rearing the young away from the sow. One should, however, bear in mind that nearly half of the losses during the rearing period occur within the first 48 hours after birth, and thus obviously could not be affected by the new routine. More pigs are often born per litter than the sow can feed, the number being limited to the number of functioning teats. At present pigs in excess of functioning teats are usually destroyed, but with artificial rearing this would, of course, not be necessary. Moreover, it may be possible in the future to breed sows

capable of producing very large litters (in excess of 12), thus increasing considerably the productivity of individual sows.

TABLE 2.11

COMPOSITION OF A SOW'S MILK SUBSTITUTE WHICH GIVES SATISFACTORY RESULTS WITH PIGS REARED "ARTIFICIALLY" AFTER INGESTION OF COLOSTRUM FOR AT LEAST 48 HR. AFTER BIRTH
(according to Johnson, James and Krider, 1948)

Ingredients	*Per cent*	*Ingredients*	*Per cent*
Casein (vitamin free)	30·0	Salts	6·0
Cerelose	37·4	Vitamins	—
Lard	26·6		
Composition of the salt mixture	*Per cent*	*Vitamins*	*Per litre*
CaHPO	33·80	Vitamin A	1·000 i.u.
K_2HPO_4	25·80	Vitamin D	100 i.u.
$CaCO_3$	22·90	Vitamin E	1 mg.
NaCl	11·85	Vitamin K	0·26 mg.
$MgSO_4$	3·50	Thiamine chloride	0·65 mg.
Ferric Citrate, $6H_2O$	1·91	Riboflavin	1·30 mg.
$MnSO_4$	0·10	Pyridoxin chloride	0·65 mg.
KI	0·06	Nicotinic acid	2·6 mg.
CaF_2	0·03	Ca-Pantothenate	7·8 mg.
$CuSO_4.5H_2O$	0·02	Inositol	26·0 mg.
$ZnCl_2$	0·02	Choline	260·0 mg.
$CoCl_2$	0·01	Paraminobenzoic acid	2·6 mg.
		Folic acid	52 µg.
		Biotin	10 µg.

2. *Heavier and more uniform pigs at 8 weeks of age.* At present the growth of pigs is limited by the amount of milk the sow can supply to them. By removing the restriction on quantity, and naturally the milk substitute can be fed *ad libitum*, heavier pigs can be obtained. In future it may be possible to produce pigs weighing on the average 60–70 lb. at 8 weeks old instead of the present average of about 30–35 lb. The litter reared on a sow frequently lacks uniformity, this often being due to the variation of milk yield from different teats. Milk substitutes will overcome this difficulty.

3. *No runt pigs.* The great majority of runt pigs are the result of shortage of milk in one or more of the teats, a disadvantage which will not exist when pigs are reared artificially.

4. *Absence of set-backs usually experienced during the normal suckling and the immediate post-weaning periods.* The lactation yield of a sow reaches its peak during the second to third week (see lactation curves, p. 48). Usually this coincides with the piglets starting to take solid food. However, the intake of the latter is not

sufficient to cover the increasing requirements for nutrients, and consequently, the growth is temporarily slowed down. Similarly, at weaning, when the milk supply is suddenly cut off, the piglets suffer a set-back. It has also been observed that around the third and the sixth week of lactation a set-back occasionally occurs, the cause of which is unknown. It is possible that it may be connected with the oestrus cycle of the sow. All these set-backs would be avoided in artificial rearing.

5. *Possibility of producing more than two litters per year per sow.* In theory, when the litter is weaned 48 hours after farrowing and the sow is mated very soon afterwards, each sow could produce three litters per year instead of the two normally produced by her, when the orthodox method of rearing is followed. However, it has already been established that, though there is no difficulty in mating the sow soon after farrowing, she will not conceive at that time. The heat is a false one at which no ovulation occurs. The subsequent heat is a true one, and it appears that a sow can conceive within three weeks of farrowing. It is conceivable, therefore, that when artificial rearing is practised, each sow may produce about five litters in two years.

6. *Complete control of the ingredients of the milk substitute, resulting in optimal supply of nutrients to the young pig.* As one example of opportunities afforded in this direction, one may quote the fact that sow's milk contains insufficient iron to satisfy the requirements of a growing pig. The milk substitute can, of course, contain as much iron as necessary.

7. *Better desease control.* The diseases which can be transmitted from the sow to her offspring would be avoided.

8. *No necessity for additional feeding of sows during lactation,* thus reducing the cost of keeping the sow.

9. *A great saving in cost and labour in cases of sows giving birth to a very small litter.* In the orthodox method of rearing such a litter requires as much attention as a normal sized one, and from the economic view point it becomes a liability rather than an asset. With artificial rearing, the size of a litter is of no consequence.

10. *Earlier marketing of sows.* If desired, the sow can be marketed satisfactorily soon after the pigs are taken away from her, a procedure which is not possible in the orthodox method of rearing. A sow which does her litter well is usually very run down at the time of weaning. Cases are known when sows have lost as much as 100 lb. in weight during the suckling period. This loss of weight will be avoided by terminating the lactation early.

The future of artificial rearing depends on a satisfactory solution to several important problems : 1. There is a serious danger of a shortage of raw materials for making milk substitutes, unless ingredients different than those used at present can be satisfactorily employed. At present, the substitutes are based on cow's milk solids. These are not available everywhere in excess of the requirements for human consumption, and their cost, high already, may become prohibitive. 2. Will the rearing on milk substitutes prove to be more advantageous than the orthodox method of rearing, when the latter is improved in the light of our present knowledge of the management and nutritional requirements of young pigs? 3. Will artificial rearing be as good a foundation for fattening as the orthodox one? 4. Will it be possible to maintain in large scale commercial practice the very high standard of management, labour and sanitation, which are the mainstay of the pioneering enterprises, and which appear to be essential to their success?

In *Figure 2.3* average growth curves are presented for pigs belonging to the same litter, one curve representing pigs reared on a sow, while the other represents pigs reared artificially. It is interesting that up to the age of about three weeks both lots of pigs grew at about the same rate, and only afterwards their growth curves separated. It appears that when pigs are reared on a sow the supply of milk is insufficient to enable them to grow at their full potential rate, particularly from the age of 2–3 weeks. Both lots of pigs received the same creep feed, and therefore one can conclude that the milk substitute fed *ad lib.* satisfied a nutritional requirement not catered for by the limited amount of milk the sow was giving to the pigs. This very point was proved recently by the Wisconsin workers, when they found that artificially reared pigs receiving sow's milk *ad lib.* grew at a similar rate to pigs receiving milk substitutes. This finding established that the quantity of milk obtained during the rearing period is the governing factor of the pigs' growth.

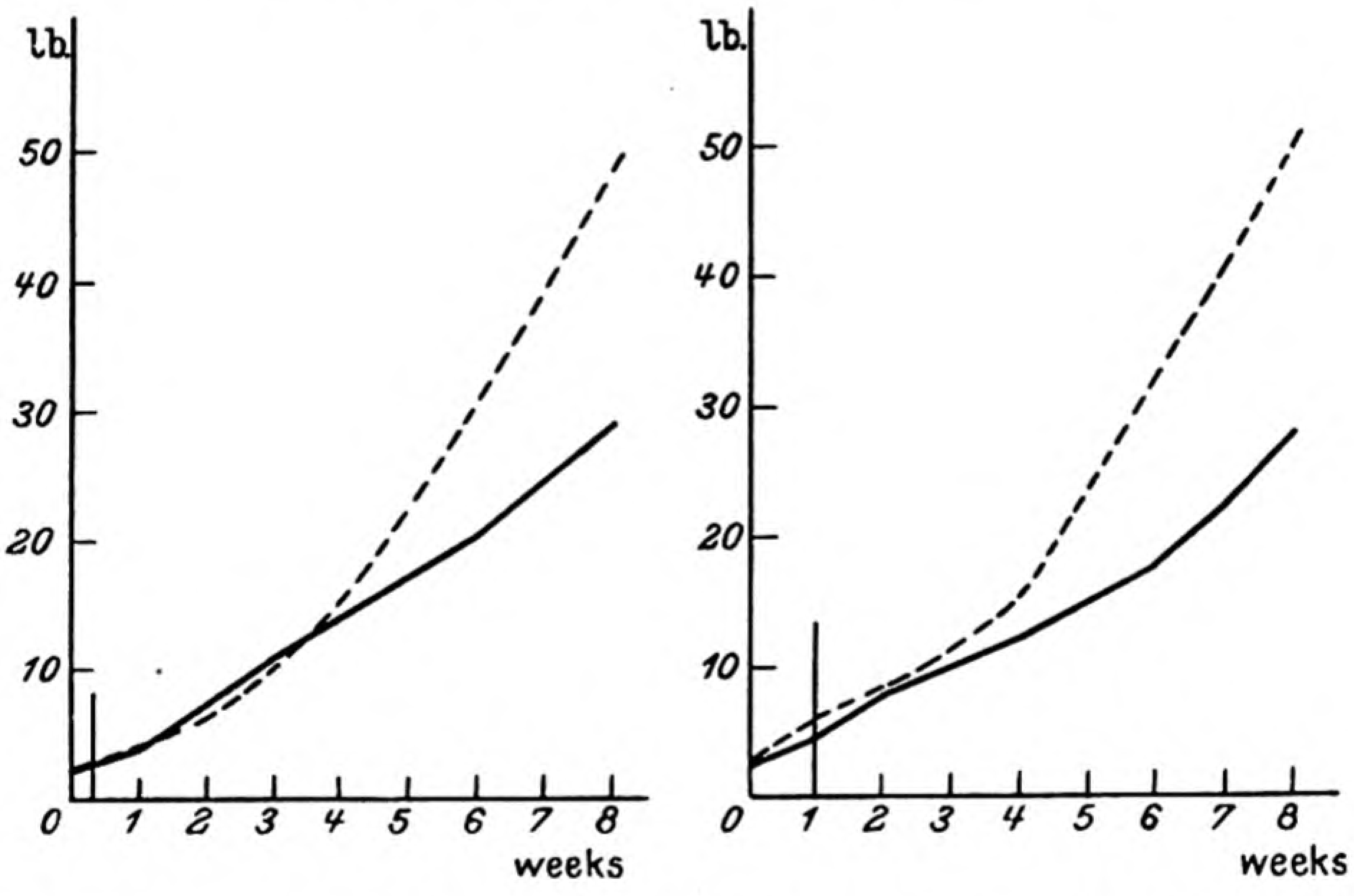


Figure 2.3. Growth curves for litter mates reared artificially (broken line) compared with those reared on the sow (full line) (Braude, unpublished data).

Quite independently of the possibility of artificial rearing of pigs becoming a generally accepted procedure, several fairly recent developments aim at improving the bringing up of young pigs :

1. A properly constructed farrowing crate has been found very useful for reducing losses in very young pigs :

2. The advantages from providing a creep in the pens where sows and their litters are kept, are now generally recognized. The installation of an additional source of heat was also found useful. Infra-red lamps are now available for creeps. There is no definite evidence available of the value of the infra-red rays for the pigs. A combination of heat and light is to be preferred to heat alone, because the light attracts the attention of the piglets when they are very young and directs them to the warmer spot. The mechanism regulating body temperature is not fully developed in a new born pig, and during the first 30 minutes after birth its body temperature may drop as much as 12°F. Recently, Newland, McMillen and Reineke (1952) studied the temperature adaptation in the baby pig, and *Figure 2.4* gives the summary of their results. The extent of drop in, and the length of time required to re-establish the normal body temperature, is directly related to the environmental temperature. Baby pigs are very sensitive to a cold environment. The size of the pig at birth, the time between birth and first suckling, the milking ability of the sow, are some of the factors affecting the post-natal drop in the body temperature of the very young pig. Provision of artificial heat will, in many circumstances, prevent this drop.

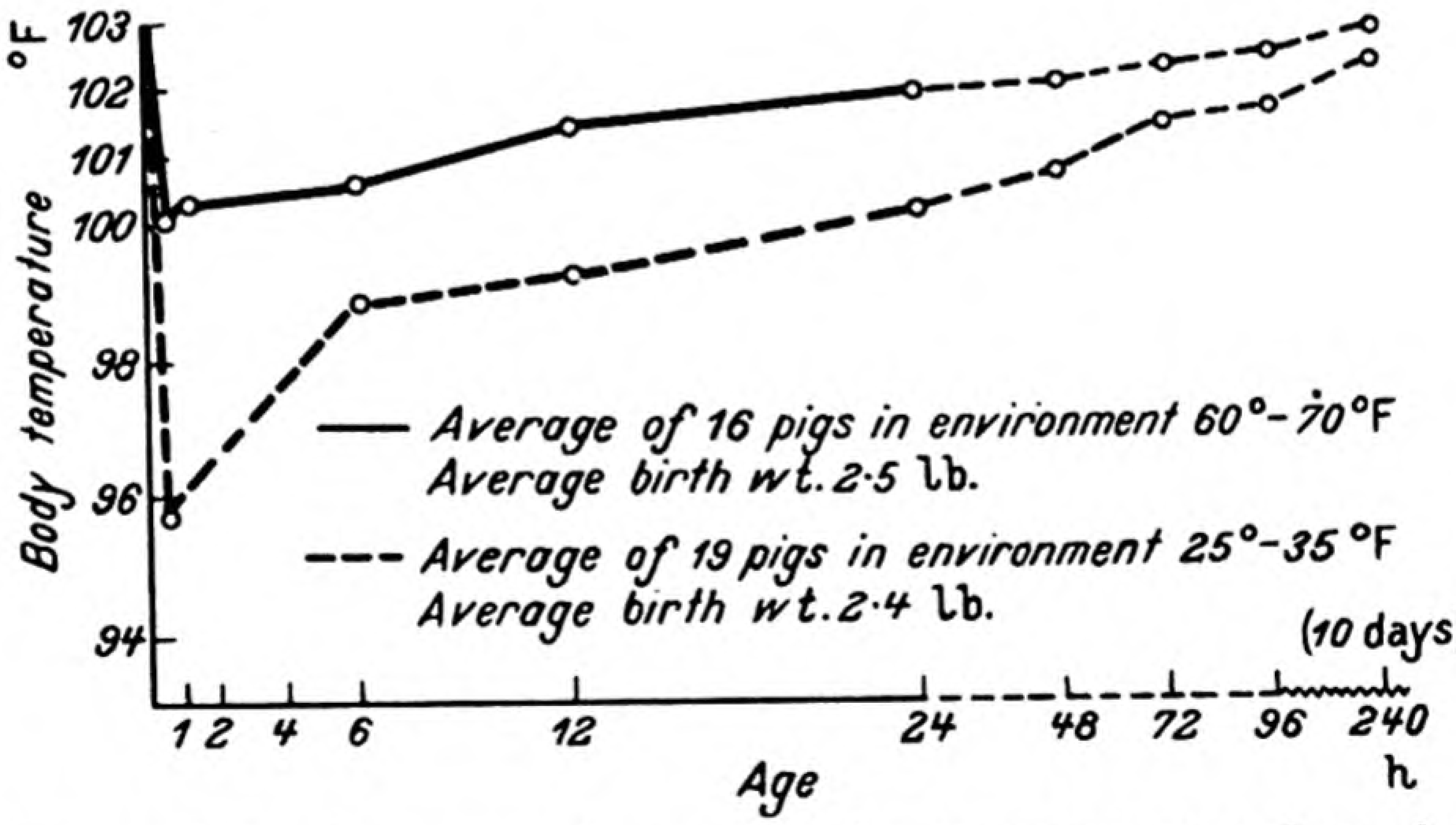


Figure 2.4. A comparison of body temperatures drop in pigs raised in warm and cold environment. (According to Newland, McMillen and Reineke, 1952.)

3. Measures to prevent anaemia in pigs reared indoors are now generally recognized as necessary, and various methods of supplying iron to the pigs are practised. In general, one could say that it is quite immaterial which of the methods is followed, provided sufficient iron finds its way into the pig. Dosing with solutions containing readily available iron—pyrophosphate, citrate or sulphate—is commonly employed. The dosing should commence when the pigs are 3–4 days old and continue for 3–6 days. Capsules of reduced iron are also efficient, one capsule being given during the first week followed by another a fortnight or so later. Smearing of the sow's udder with a solution containing iron is rapidly going out of favour, and so is the provision of soil in indoor pens. The efficacy of the most recent method, namely a single intramuscular injection of iron, is not yet proved.

4. The importance of nutritionally adequate meal mixtures for suckling pigs is gradually being recognized. Our present knowledge of the actual nutritional requirements of a suckling pig is very limited, but a number of satisfactory formulas have been arrived at empirically. These formulas are usually rather complicated, and provide the essential nutrients in quantities allowing a large margin of safety. The three essential features for a satisfactory creep mixture are : a high protein content—20–22%, as low fibre content as possible, and high palatability. Table 2.12 gives examples of two creep meal mixtures.

TABLE 2.12

EXAMPLES OF CREEP MEALS FOR PIGS

American creep meal mixed by compounder	*Per cent*	*British creep meal mixed on farm*	*Per cent*
Rolled oats	50	Barley meal	22
Soya bean oil meal	20	Wheat offal	20
Maize meal	15	Flaked maize	20
Sugar	7·5	Dried skim milk	15
Fish meal	2·5	White fish meal	15
Dried whey	2·5	Dried grass	5
Steamed bone meal	1·0	Dried yeast	3
Ground limestone	0·75		
Salt	0·5		
Trace mineral	0·25		
+ the following vitamins per 100 lb.			
Vitamin A	300,000 units	Nicotinic acid	3 g.
Vitamin D	50,000 units	Calcium pantothenate	300 mg.
Vitamin B_{12}	2 mg.	Choline chloride	7·5 g.
Riboflavin	300 mg.	Antibiotic	2 g.

The creep meals should be made available to the piglets when they are about 10 days old. Many pigs will start nibbling at supplementary food as soon as it is introduced. Others may not touch it until they are much older, but an opportunity should be given to them to start as early as possible. It is important to make the creep feed most attractive to the piglets. Baby pigs like hard particles which they can crack between their teeth, so the inclusion of flaked maize into creep meal mixtures is often recommended. Another way of catering for this liking is to supply pellets instead of meal. Also, an addition of a small amount of sugar, in the form of syrup or molasses, to the creep feed, appears to improve the palatability of the mixture.

It has been generally recognized that litters reared out-of-doors, on grass, do better than those reared indoors. This fact has been recently confirmed by the results of a large-scale test carried out at Shinfield, presented in Table 2.13. These results point to two definite conclusions: (*a*) The better growth of piglets reared out-of-doors is associated with their access to actively growing vegetation and to soil. (*b*) The piglets on grass grew better because they started to eat creep feed earlier and ate much more of it than pigs reared indoors (BARBER, BRAUDE and MITCHELL, 1953a). The factor responsible for inducing the pigs to eat more is as yet unknown.

TABLE 2.13

RESULTS OF AN EXPERIMENT IN WHICH INDOOR *v.* OUTDOOR REARING OF PIGS WAS COMPARED

(according to Barber, Braude and Mitchell, 1953a)

Management system	*No. of litters*	*Pigs born alive*		*Average birth weight (only pigs which survive 8 weeks)*	*Pigs weaned at 8 weeks old*			*Average weight at weaning lb.*	*Average amount of meal consumed per pig lb.*
		Total No.	*No. per litter*		*Total No.*	*No. per litter weaned*	*% of pigs born alive*		
Indoors	20	239	11·95	2·68	193	9·65	80·8	26·62	8·54
Outdoors on concrete	20	223	11·15	2·58	192	9·60	86·1	26·04	11·41
Indoors with soil	14	162	11·57	2·59	129	9·20	79·6	28·09	12·38
On grass	20	244	12·20	2·62	206	10·30	84·4	32·30	19·43

In recent years many commercial piggeries suffered heavily from losses of baby pigs dying within a few days after birth. There is, at present, no general explanation available which would satisfactorily cover all these deaths. Occasionally, hypoglycaemia is mentioned in this connexion. Hypoglycaemia develops rapidly if piglets are short of food, for whatever reason. The piglets usually succumb to it, after a brief period of loss in body weight and lowered body temperature. The condition can be prevented by glucose. The rate of development of critical hypoglycaemia depends on environmental temperature. High temperatures are helpful as they conserve the natal carbohydrate reserves through reduction in rate of heat loss.

NUTRITIVE REQUIREMENTS OF PIGS

ENERGY AND PROTEIN

Most of the fundamental work on the nutritional requirements of the pig has been carried out on the growing-fattening animal. It is recognized that to feed a pig satisfactorily a balanced diet supplying energy, protein, minerals and vitamins, is essential, and in the following pages our present-day knowledge concerning these four groups of nutrients will be discussed.

Table 2.14

DAILY FOOD REQUIREMENTS AND HEAT PRODUCTION OF GROWING AND FATTENING PIGS

(according to Mitchell and Kelley, 1938)

Body weights	*Average daily gain*	*Total net energy required*	*Metabolizable energy required*	*Dry matter required*	*Feed economy of gains**	*Total heat produced*
lb.	*lb.*	*Cal.*	*Cal.*	*lb.*	*lb.*	*Cal.*
2·5	0·15	268	359	0·24	1·8	209
5	0·23	444	593	0·39	1·9	375
10	0·37	719	954	0·63	1·9	651
25	0·65	1,285	1,688	1·11	1·9	1,233
50	0·97	1,887	2,462	1·62	1·9	1,783
75	1·25	2,422	3,207	2·11	1·9	2,207
100	1·50	3,098	4,141	2·73	2·1	2,641
125	1·73	3,929	5,282	3·48	2·3	3,206
150	1·95	5,035	6,813	4·57	2·6	3,908
175	2·03	5,756	7,812	5·14	2·9	4,361
200	1·95	6,354	8,639	5·68	3·3	4,739
225	1·75	6,955	9,475	6·24	4·0	5,100
250	1·55	8,115	11,113	7·31	5·4	5,688

* Expressed in lb. food (containing 12 per cent of moisture) required per pound of gain.

Basing themselves on data from Breirem (1935), Brody *et al* (1932), Deighton (1929, 1935), Mitchell *et al* (1931), and Wood (1926), Mitchell and Kelley (1938) have calculated and tabulated the energy requirement of pigs of various ages, which include requirements for growth, reproduction and lactation. Tables 2.14, 2.15 and 2.16 give the appropriate values. Table 2.14 refers to British conditions of pig husbandry. One should refer back to the original paper for values calculated for the American conditions. Although these values are based on extensive experimental data, many assumptions had to be made before arriving at the average figures. Being the best available at present, they are nevertheless tentative, and must await confirmation from further fundamental studies.

The total energy requirements include both the energy for maintenance and for production, the latter being either growth, reproduction

TABLE 2.15

DAILY FOOD REQUIREMENTS OF A PREGNANT SOW WEIGHING 400 LB.
(according to H. H. Mitchell, unpublished data)

Week of gestation	*Body weight**	*Total net energy required*	*Total metabolizable energy required†*	*Total dry matter required*	*Total protein required in % of dry matter‡*
	lb.	*Cal.*	*Cal.*	*lb.*	
0	400	5,270	6,968	4·38	7·9
1	406	5,273	6,968	4·38	7·8
2	411	5,261	6,954	4·38	7·8
3	417	5,301	6,994	4·40	7·9
4	424	5,337	7,035	4·43	7·7
5	429	5,349	7,047	4·43	7·8
6	436	5,363	7,062	4·44	8·1
7	443	5,379	7,079	4·45	8·2
8	450	5,428	7,138	4·49	8·1
9	456	5,478	7,199	4·53	8·6
10	464	5,531	7,264	4·57	8·6
11	471	5,597	7,346	4·62	8·9
12	478	5,656	7,415	4·67	8·9
13	486	5,684	7,452	4·69	9·2
14	493	5,817	7,618	4·80	9·5
15	501	5,943	7,777	4·89	9·6
16	509	6,116	7,992	5·03	10·1

* Includes growth of maternal organism and growth of total products of conception.

† Assuming 80 per cent net availability of metabolizable energy for maintenance and 70 per cent for growth, both maternal and foetal.

‡ Assuming a coefficient of apparent digestibility of protein of 77 per cent.

TABLE 2.16

DAILY FOOD REQUIREMENTS OF A LACTATING 400 LB. SOW, FED TO MAINTAIN BODY WEIGHT
(according to Mitchell and Kelley, 1938)

Week of lactation	*Milk produced daily*	*Total net energy required*	*Metabolizable energy required*	*Dry matter required*
	lb.	*Cal.*	*Cal.*	*lb.*
0	0·0	3,150	3,937	2·6
First	6·57	7,447	9,309	6·1
Second	7·86	8,290	10,363	6·8
Third	8·29	8,572	10,715	7·0
Fourth	8·00	8,382	10,477	6·9
Fifth	7·43	8,009	10,011	6·6
Sixth	6·57	7,447	9,309	6·1
Seventh	5·86	6,982	8,728	5·7
Eighth	5·14	6,512	8,140	5·3

or lactation. The energy requirements for maintenance include the energy needed to maintain the circulation, respiration, digestion and excretion, and energy associated with muscle tension, activities of the enzyme systems and the thermodynamic processes of life. The maintenance requirements, though quite large, are difficult to assess experimentally. However, a number of workers attempted to establish the maintenance requirements of energy for growing pigs, and Table 2.17 summarizes the results obtained.

TABLE 2.17

COMPARISON OF DIFFERENT ESTIMATES OF DAILY MAINTENANCE ENERGY REQUIREMENTS OF PIGS (Cal.)

Weight of pigs lb.	*Deighton (1929)*	*Breirem (1935)*	*Edin and Helleday (1935)*	*Brody et al (1932)*	*Mitchell and Hamilton (1929)*
50	1,410	930	1,167	1,370	1,320
100	2,250	1,370	1,980	2,280	2,370
150	2,720	1,720	2,400	3,060	3,290
200	2,960	2,010	2,470	3,790	3,950
250	3,110	2,280	—	4,400	3,950

The energy requirements for growth, as presented by Wood (1926), are given in *Figure 2.5*, which shows the caloric value of successive increments of live weight, based on English feeding practices. Values calculated by Mitchell and Kelley (1938), based on American data, are considerably higher. Both, however, show clearly that the energetic efficiency of growth decreases with the growth of the animal. This is due to the fact that maintenance requirements increase in relation to the weight gain. Table 2.18, taken from Mitchell and Kelley (1938), gives the estimated energy content of a pound of gain for pigs of different body weights.

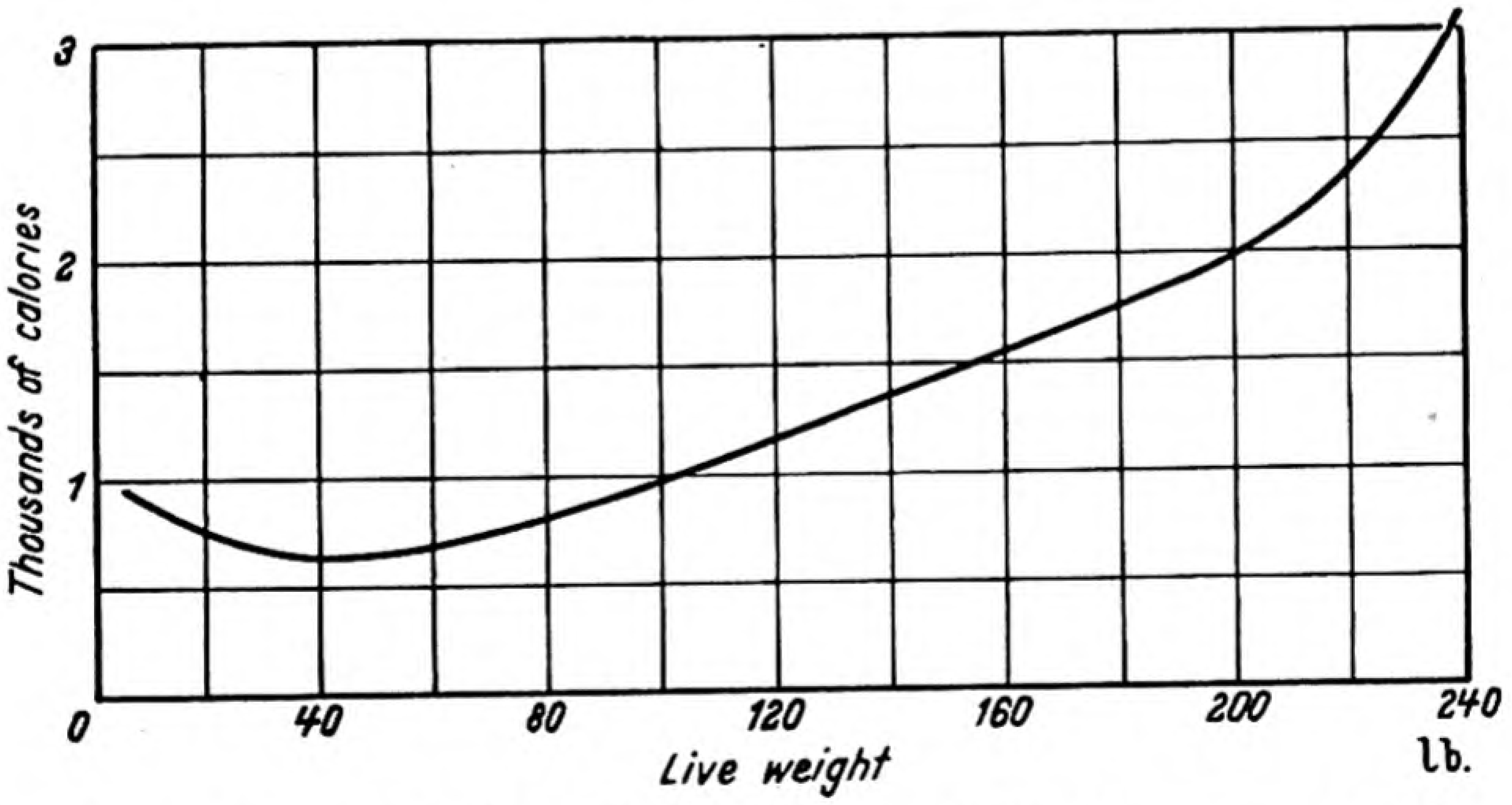


Figure 2.5. Caloric value of live weight increase per lb. (According to Wood, 1926).

TABLE 2.18

ESTIMATED ENERGY CONTENT OF A POUND OF GAIN BY PIGS OF INCREASING BODY WEIGHT

(according to Mitchell and Kelley, 1938)

Body weight	*Energy content of gain per lb.*	*Body weight*	*Energy content of gain per lb.*
lb.	*Cal.*	*lb.*	*Cal.*
2·5	500	175	2,200
5	750	200	2,400
10	1,000	225	2,600
25	1,250	260	2,850
50	1,500	300	3,200
75	1,625	400	3,750
100	1,750	500	3,950
125	1,850	600	4,050
150	2,025		

As the pig gets older, the chemical composition of its body changes and *Figure 2.6*, taken from Wood (1926), shows the changes in fat and protein content of pig carcasses at varying ages. A different trend is shown in Table 2.19, taken from BULL and CARROLL (1946), which gives the average composition of pigs at different ages. With age, the percentage of water, protein and ash in the carcass decreases, while that of fat increases very markedly. Wood (1926) has estimated that the amount of energy required for the production of 1 lb. of fat is 4,268

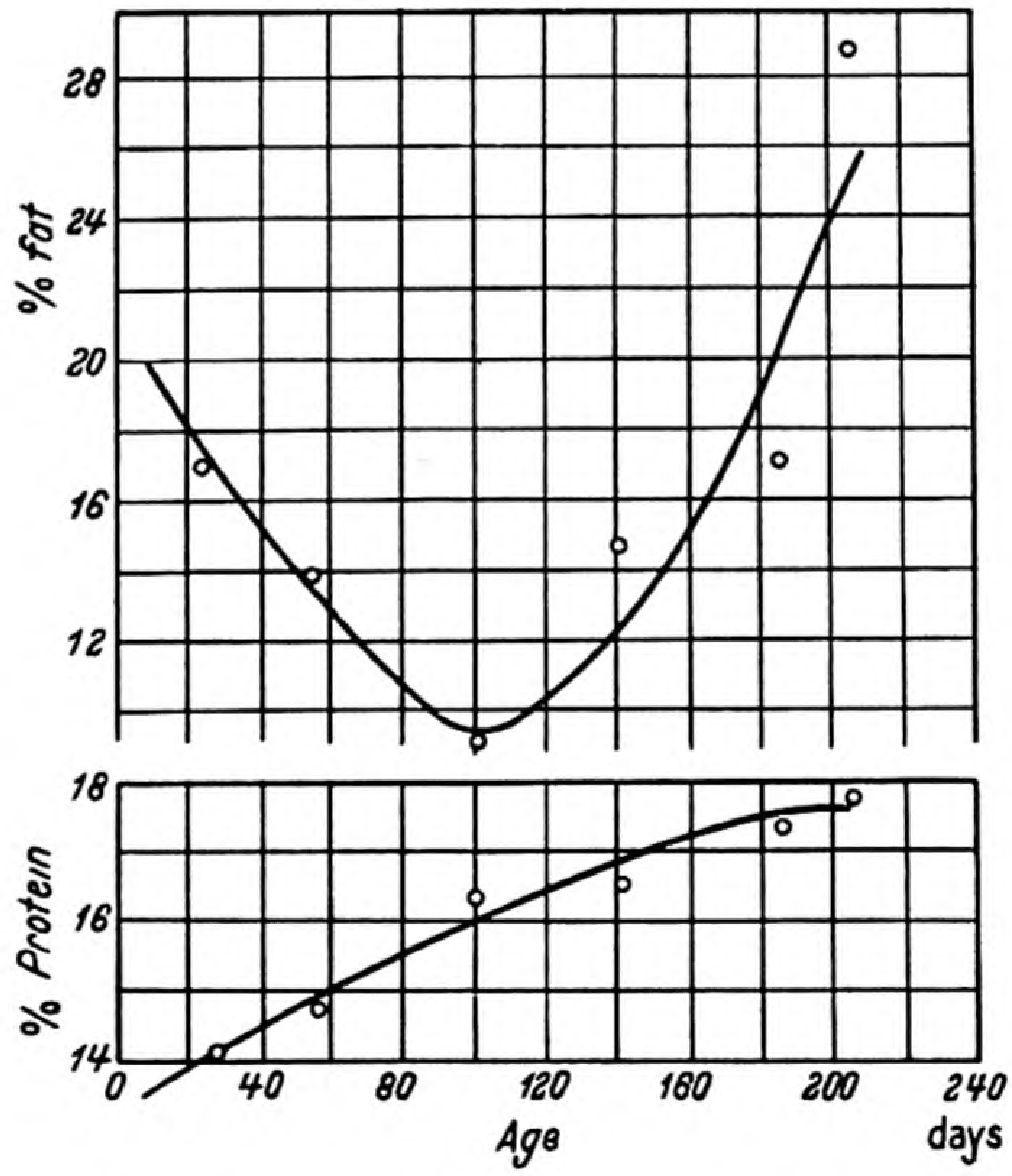


Figure 2.6. Changes in fat and protein content of pig carcasses (empty weight) at varying ages (according to Wood, 1926).

calories, while that for 1 lb. of protein is 2,633 calories only. It thus becomes obvious why a young pig is so much more efficient in utilizing its food for growth than an older one. As soon as the animal begins to deposit fat at an increased rate, the amount of energy it requires per unit of gain also increases.

TABLE 2.19

AVERAGE COMPOSITION OF THE PIG

(according to Bull and Carroll, 1949)

	No. of pigs analysed	*Water* %	*Protein* %	*Fat* %	*Ash* %
At Birth	4	79·7	14·2	2·0	4·1
15 days old	7	65·9	13·9	17·3	3·1
35 days old	7	69·7	14·2	13·0	3·4
55–70 lb.	30	63·9	12·3	20·3	2·3
175 lb.	12	52·1	11·5	33·6	2·4
225 lb.	58	51·5	11·6	34·9	2·1
275 lb.	10	45·2	11·0	40·9	2·2
300 lb.	2	41·1	11·4	41·5	2·0

The same point, differently approached, is made by McMEEKAN (1941), who showed that the skeleton, muscle and fat exhibit marked differential growth. The skeleton, developing first, makes a greater proportion of its growth earlier in life than does the muscle, whilst the latter makes the greater proportion of its growth earlier than does the late developing fat. In his classic experiment, with different planes of nutrition, McMeekan has demonstrated that the earlier developing parts have a prior claim to the available supplies of nutrients. By quantitative control of the plane of nutrition, pigs were made to conform to four major variations in the shape of growth curve from birth to 200 lb. live weight. Pigs from an inbred strain of the Large White breed were reared from birth to 16 weeks on a High Plane and a Low Plane of nutrition respectively, using qualitatively identical rations. At 16 weeks a change in the treatment of some of them was introduced. While some of the High Plane and some of the Low Plane pigs continued on their respective rations until they attained a weight of 200 lb., the treatment of the remaining animals was reversed. Some High Plane animals were changed to a Low Plane, and some Low to a High Plane of nutrition, and their growth controlled in such a way that individual pairs on each treatment reached 200 lb. live weight at the same age. *Figure 2.7* gives the plan of McMeekan's experiment. The results were summarized by McMeekan, as follows: "The results obtained afford convincing evidence of the influence of nutritional requirement as a directive and controlling force in the development of the animal body. In body form two distinct types of pigs were used. The High-high and the Low-high pigs were similar with greater proportional development of the late developing parts of the body. Compared with these, the High-low and the Low-low showed proportionally greater development of the early developing parts. Within each type, the animal subjected to inadequate nutrition in early life showed the effects noted to a relatively greater extent. Even more striking effects were produced on the major body tissues. The amount of skeleton and muscle increased, and fat decreased in the following order: Low-high, High-high, High-low and Low-low. Mean treatment differences relative to Low-low ranged from 6–20% less in bone, 5–25% less in muscle, and 26–64% more in fat". It is quite impossible to summarize here all the other findings of McMeekan, but those interested in growth and development in the pig are well advised to study his treatise in detail.

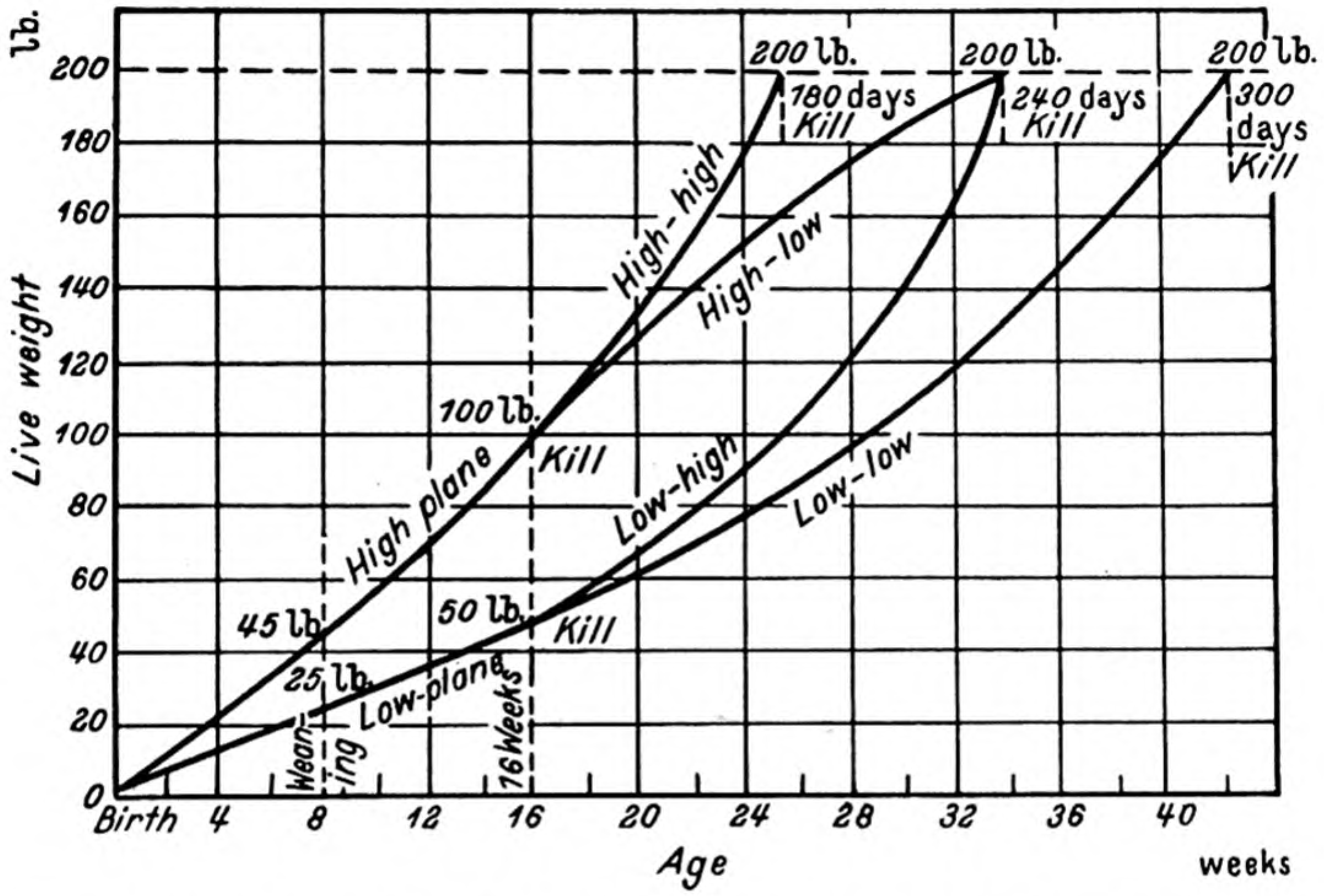
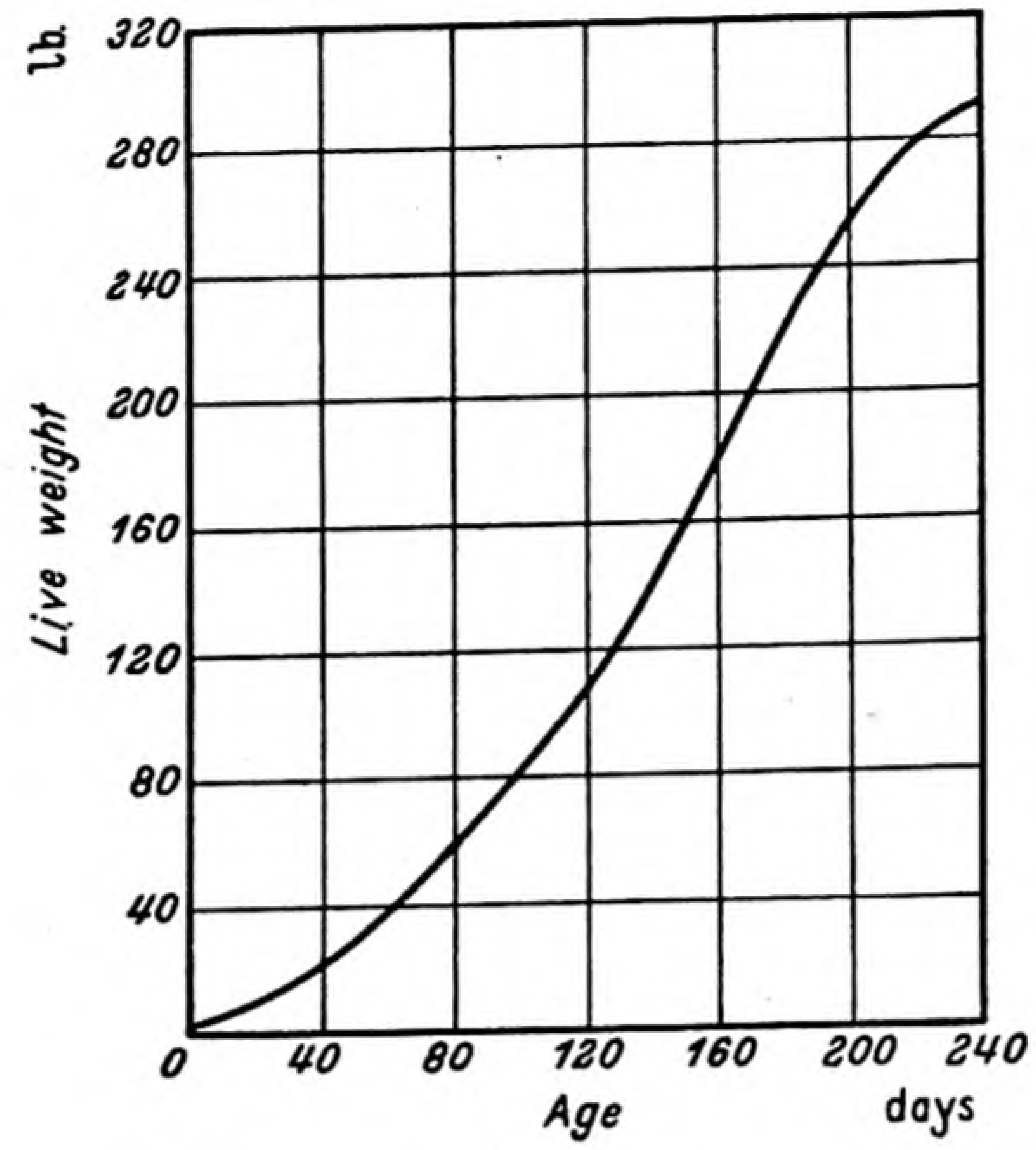


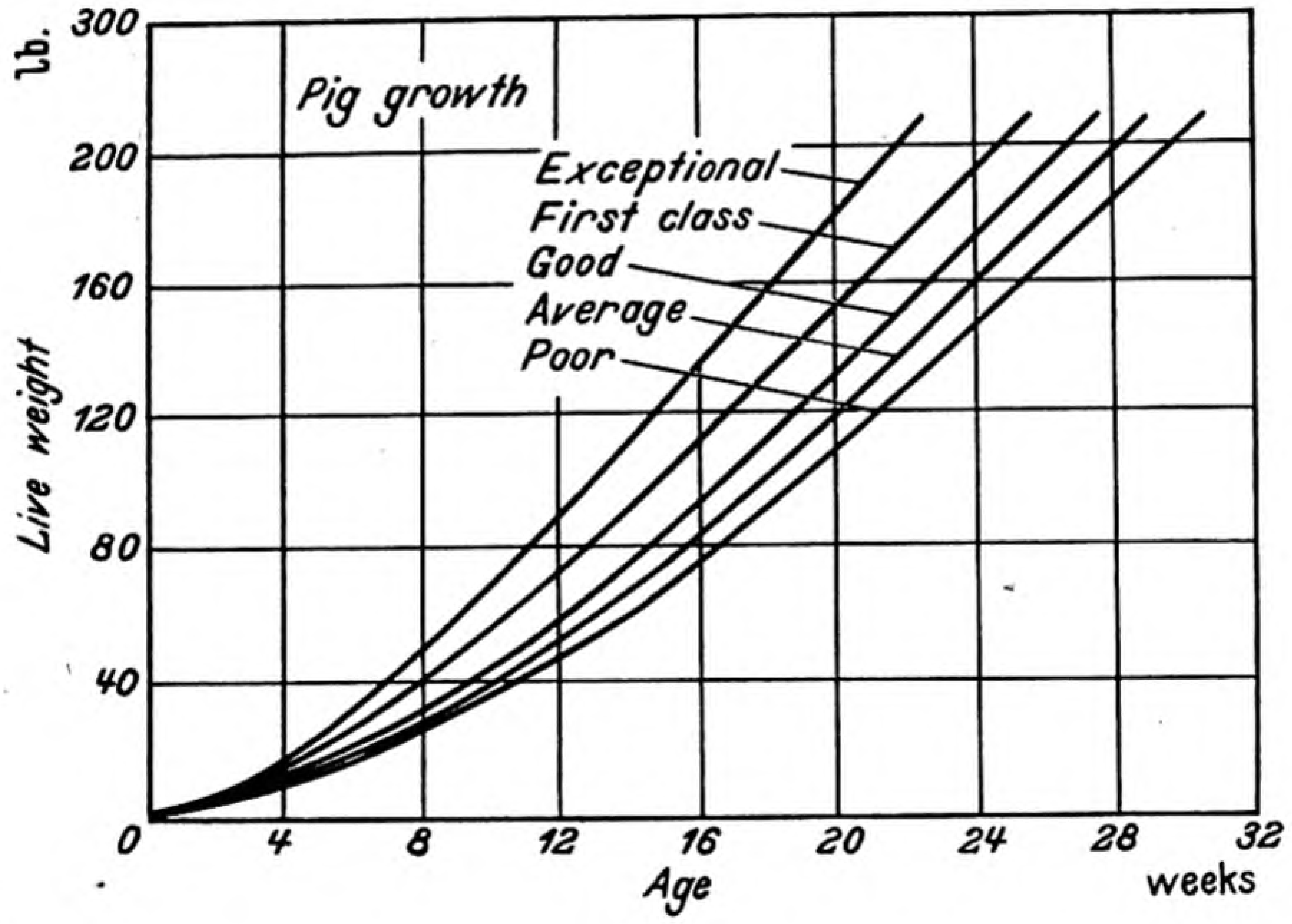
Figure 2.7. Plan of McMeekan's experiment to determine whether the composition and conformation of the pig can be changed by altering the shape of its growth curve (McMeekan, 1941).

Figure 2.8a gives a typical growth curve for pigs. It is evident that after the animals attain a certain size, the slope of the growth curve is changed. A similar tendency can be seen from the values in column 2 of Table 2.14. The maximum rate of gain is attained when a pig weighs 150–200 lb. When judging the economy of production, the variation in the growth rate with age must be considered in conjunction with the values for the efficiency of food utilization (Table 2.14, column 6). The efficiency with which a pig utilizes food declines rapidly, as the animal grows older.

Figure 2.8b gives growth curves which are based on the varying growth rates encountered in practical pig keeping.



(*a*)



(*b*)

Figure 2.8. (*a*) Growth curve of pigs. (*b*) Growth curves of pigs growing at varying rates under practical pig keeping conditions.

Several authorities throughout the world have recommended feeding standards for growing–fattening pigs. In Table 2.20 the recommendations of the (U.S.A.) National Research Council (1950) are reproduced. These are average figures adjusted to the American conditions of pig husbandry. However, with only slight modifications, these values are generally applicable. Further details can be obtained from the original works of Axelson (1949), Breirem (1935), Edin and Helleday (1935), Fraps (1943), Hanssen and Bengtson (1930), Kellner (1905), Mitchell and Hamilton (1929), and Morrison (1936).

TABLE 2.20

NUTRIENT ALLOWANCES FOR PIGS

(according to Recommendations of the National Research Council, 1950)

Description of pigs			*Energy and protein*				*Total crude protein per lb. ration lb.*
			Daily allowances			*Digestible nutrients lb. per diet lb.*	
Class	*Live weight*	*Expected daily gain*	*Total feed air dry basis*	*Digestible nutrients*	*Crude protein*		
	lb.	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*
Growing— fattening pigs	50	1·0	3·0	2·3	0·55	0·75	0·18
	100	1·6	5·3	4·0	0·85	0·75	0·16
	150	1·8	6·8	5·1	0·95	0·75	0·14
	200	1·8	7·5	5·6	1·00	0·75	0·13
	250	1·8	8·3	6·2	1·00	0·75	0·12
Pregnant and breeding sows	300	0·75	6·0	4·5	0·90	0·75	0·15
	500	0·5	7·5	5·6	0·90	0·75	0·12
Lactating females	350	—	11·0	8·3	1·65	0·75	0·15
	450	—	12·5	9·4	1·90	0·75	0·15

In considering feeding standards for pigs, one should beware of generalizations. Very little fundamental work was ever undertaken on a sufficiently large scale to allow any definite statements to be made. A good illustration of how misleading generalizations can be is found in the fact that Kellner's starch equivalent figures are being readily applied to pigs. The original Kellner's starch equivalent theory was based on estimations of the fat production capacity of the various nutrients, carried out in respiration tests with steers. Only very few trials were done with pigs. However, from then onwards it was generally assumed that these starch equivalent values are applicable to pigs. Kellner's successor, Fingerling, undertook large-scale respiration trials with pigs. His work was not completed when he died in 1944, and only recently his successor, Nehring (1950) published the values obtained in these tests. In Table 2.21 these values are listed and compared with the Kellner values obtained with steers. The two sets of values point to a much greater efficiency of the pig in converting various nutrients to fat ; thus it is obvious that the application of Kellner's values to pigs was based on an erroneous assumption.

As far as the protein requirements of the pig are concerned, there exists a controversy whether these requirements have not been

TABLE 2.21

FAT PRODUCTION ABILITY OF PURE NUTRIENTS

(according to Nehring, 1950)

	Fingerling's values obtained with pigs		*Kellner's values obtained with steers*	
	g. fat	*Calories*	*g. fat*	*Calories*
1 kg. starch	356	3,410	248	2,360
1 kg. sugar	281	2,670	188	1,790
1 kg. fat	880	8,360	474–598	4,500–5,685
1 kg. protein	363	3,450	235	2,240
1 kg. crude fibre*	248	2,350	253	2,400

* In the experiments with pigs—straw was used.

overstated in the past. One argument put forward is that the level at which protein supplements were included in the rations catered not only for essential nitrogenous compounds of the diet, but also for other important nutrients, such as vitamins and minerals, which often formed a part of the protein supplements. During the previous decade, the Cambridge workers, WOODMAN and EVANS (1939, 1940, 1941, 1945), produced convincing evidence that pigs grow satisfactorily on lower levels of protein than those generally recommended. More recently similar evidence was produced by CATRON *et al* (1952). The recommendations of the National Research Council took this trend into account, and the values of the 1950 edition are lower than those in the previous edition (1944), and further reductions are likely to be recommended in the next edition.

It is interesting to note that Woodman and Evans (1948) point out that at low level of intake, protein is more efficiently utilized in the body of the animal. This was confirmed by experiments of COLUMBUS (1950), who showed that when the amount of fish meal in the diet of the pig was increased from 50 g. daily to 300 g. the biological value of the fish meal first rose from 82·3 to 95·0 and then fell steadily to 71·4.

Excess of protein in the diet has actually proved detrimental to the pig. It was responsible for reduced rate of growth and lower efficiency of food utilization (ROBINSON, 1940 ; TERRILL *et al* 1952). These adverse effects are not encountered when the crude protein content of the diet is below 30 per cent, a very rare level under practical conditions. Over-feeding with protein will cause scouring, and on post-mortem examination the kidneys, liver and spleen are found considerably enlarged. Protein consumed in excess of the animal's needs cannot be stored for future use. The excess is converted into carbohydrates or burnt and dissipated as heat.

When considering reduction in the protein beyond a certain level, however, one should beware of a possibility of lowering the animal's resistance to disease. Apparently, protein is needed for the production of protective antibodies and also for the maintenance of intestinal motility and mucosal structure. Low-protein diets can be responsible for hypomotility of the small intestines, which may not only adversely affect food absorption, but also lower the local resistance of tissue to infection. In protein deficiency the production of enzymes necessary to digest and utilize food may also be impaired.

In the present state of our knowledge, the evaluation of foods as sources of protein must be viewed in terms of component amino acids, without undue emphasis on the composition of a single characteristic protein, *e.g.* zein in maize or casein in milk. However, the time may not be far ahead when the actual amino-acid composition of the pig's rations will have to be considered in detail. Studies to establish the amino-acid requirements of pigs are now being conducted and Table 2.22

TABLE 2.22

AMINO-ACID REQUIREMENTS OF PIGS

Amino acid	*Amount in the diet*	*Conditions under which applicable*	*Reference*
Tryptophan	0·4% (DL)	Adequate for 50–100 lb. pig (Optimum level unknown)	Beeson *et al*, 1949a
	0·2% (DL) 0·05% (DL)		Shelton *et al*, 1951c
	0·1% (L)	Baby pigs	Thompson *et al*, 1952
Lysine	0·6%		Brinegar *et al*, 1949
	0·6%	On ration containing 10·6% protein	
	1·2%	On ration containing 22·0% protein	Brinegar *et al*, 1950a
	2·0% (DL)	Normal growth on synthetic diet	Mertz *et al*, 1949
	0·8–1·0%	On high protein (24%) diet	Shelton *et al*, 1951b
Methionine	0·07–0·27%	On ration containing 10% protein	Bell *et al*, 1950
	0·6%	In the absence of cystine in diet	
	0·3%	In the presence of cystine in diet	Shelton *et al*, 1951a
	0·31%	On ration containing 22% protein and 0·38% cystine	Curtin *et al*, 1952b
Isoleucine	0·7% (L)	Maximum growth response	Brinegar *et al*, 1950b
Threonine	0·4% (L)		Mertz *et al*, 1952
	0·9% (L)	Baby pigs on ration containing 25% protein	Sewell *et al*, 1952 1953
Valine	0·4% (L)	—	Jackson *et al*, 1953

gives details concerning the results obtained up-to-date. As this kind of experimental evidence is not easy to obtain, it will be some time before reliable information on all the amino acids is assembled. The Cornell workers, CURTIN *et al* (1952a), however, have tried, by an ingenious short cut, to obtain this information more quickly. They have analysed various pigs' carcasses for their amino acid content, and found similar values for different age groups of pigs. Having learned the proportion of various amino acids present in the body, and having ascertained experimentally the requirement for one of the amino acids, lysine, they proceeded to calculate from these criteria the probable amino acid requirements of the growing pig. The values they arrived at are given in Table 2.23.

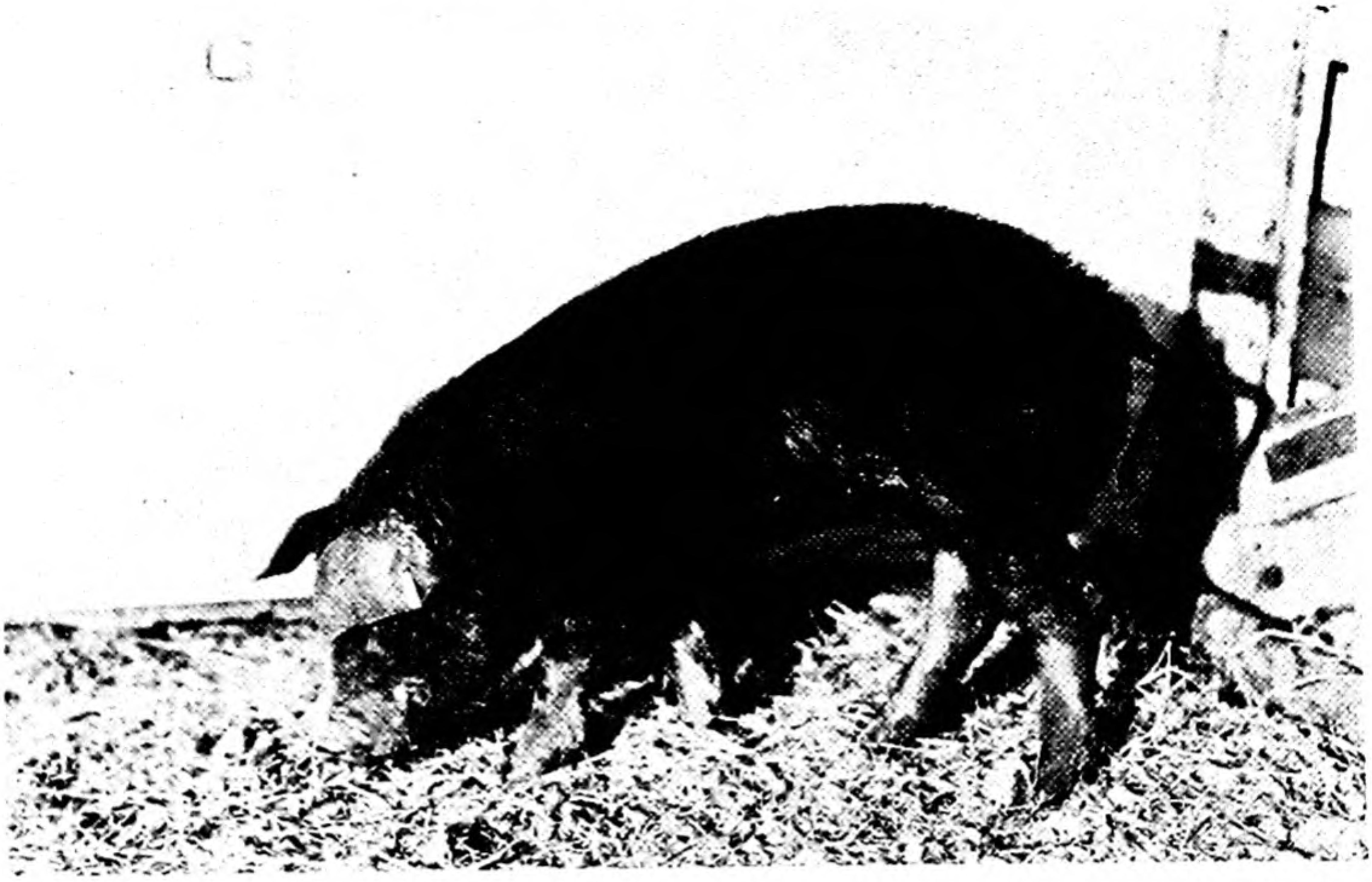
TABLE 2.23

AMINO-ACID REQUIREMENT FOR GROWTH

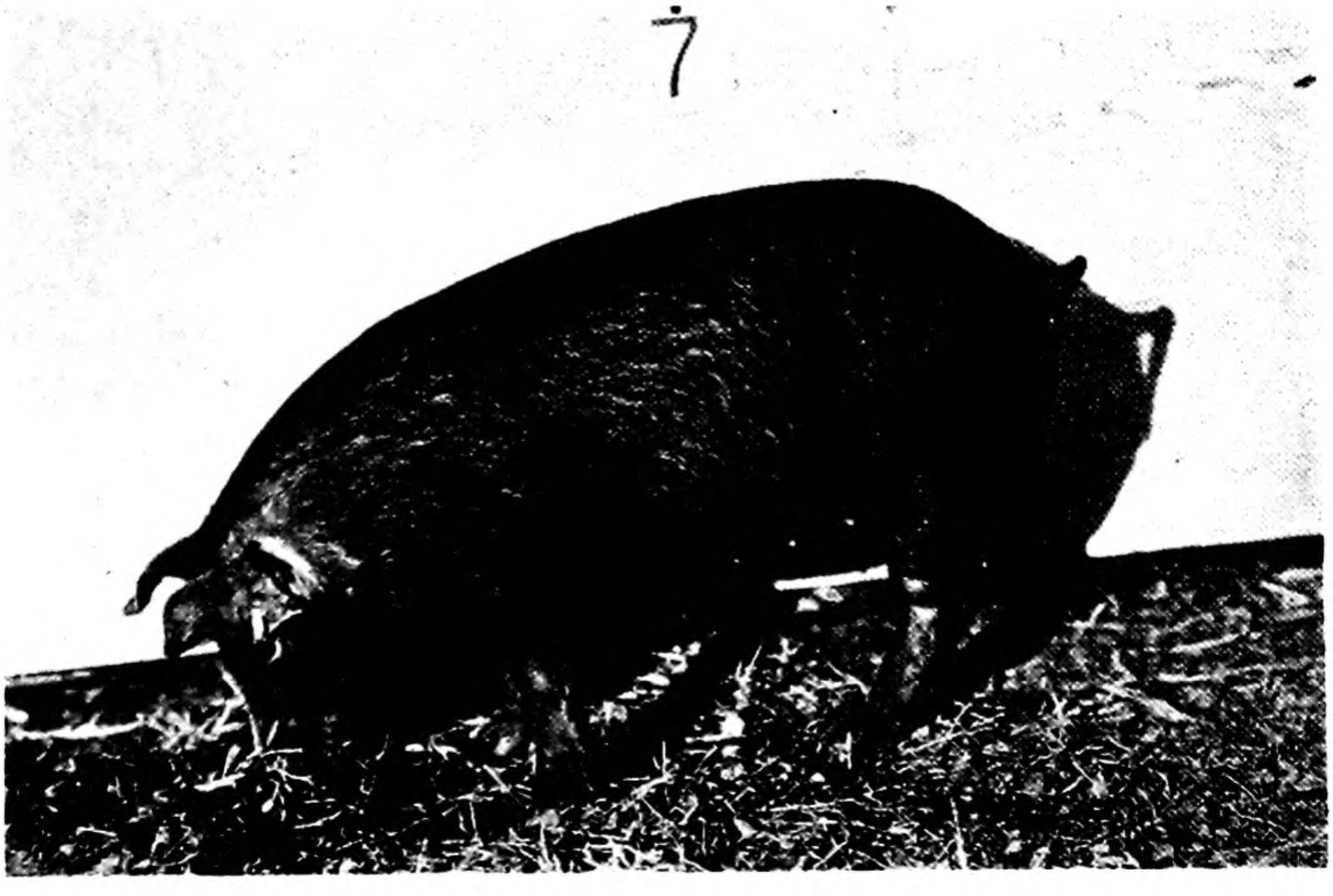
	As estimated by Curtin et al (1952a) % of protein	*Amount in purified diet giving normal growth according to Shelton et al (1950)*		*As estimated by Curtin et al (1952a) % of protein*	*Amount in purified diet giving normal growth according to Shelton et al (1950)*
Arginine	4·6	0·25	Methionine	1·2	0·60
Histidine	1·8	0·50	Phenylalanine	2·4	0·90
Isolewine	2·6	1·00	Threonine	2·4	1·00
Leucine	4·6	0·80	Tryptophan	0·5	0·20
Lysine	5·5	2·50	Valine	3·9	1·40

At about the same time Purdue workers, SHELTON, BEESON and MERTZ (1950) proved experimentally that pigs can grow normally when fed on a " synthetic diet " containing the essential amino acids as the only source of nitrogen. The amounts of amino acids which gave satisfactory growth are also given in Table 2.23.

In general, the amino-acid requirements, expressed as percentages of the diet, decrease as the growth decreases, which falls in line with the decrease with age in the protein requirements of the pig. The problem of amino-acid requirements is complicated by the possibility of interaction between various amino acids, so that the requirement for any one amino acid may depend on the quantity of other amino acids present in the ration. An amino acid which is synthesized from another becomes a dietary requirement only if there is a deficiency of its precursor. About half of the known amino acids can be synthesized from the dietary " essential " amino acids, but this synthesis by the body may be sometimes too slow to keep up with the needs for rapid growth, and retardation of the latter will therefore occur. Experimental evidence is already available to show that lack of tryptophan in the

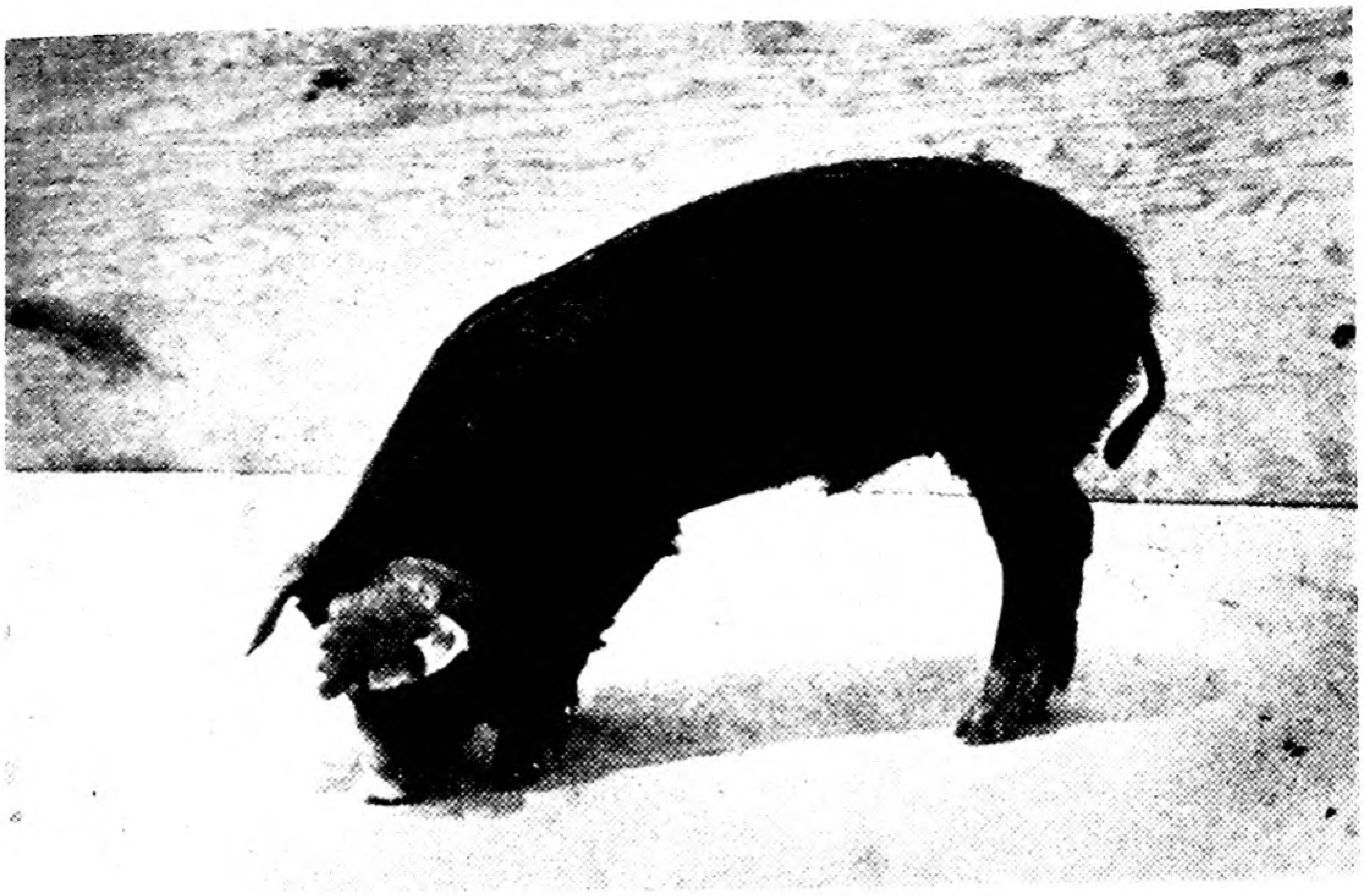


Pig No. 8

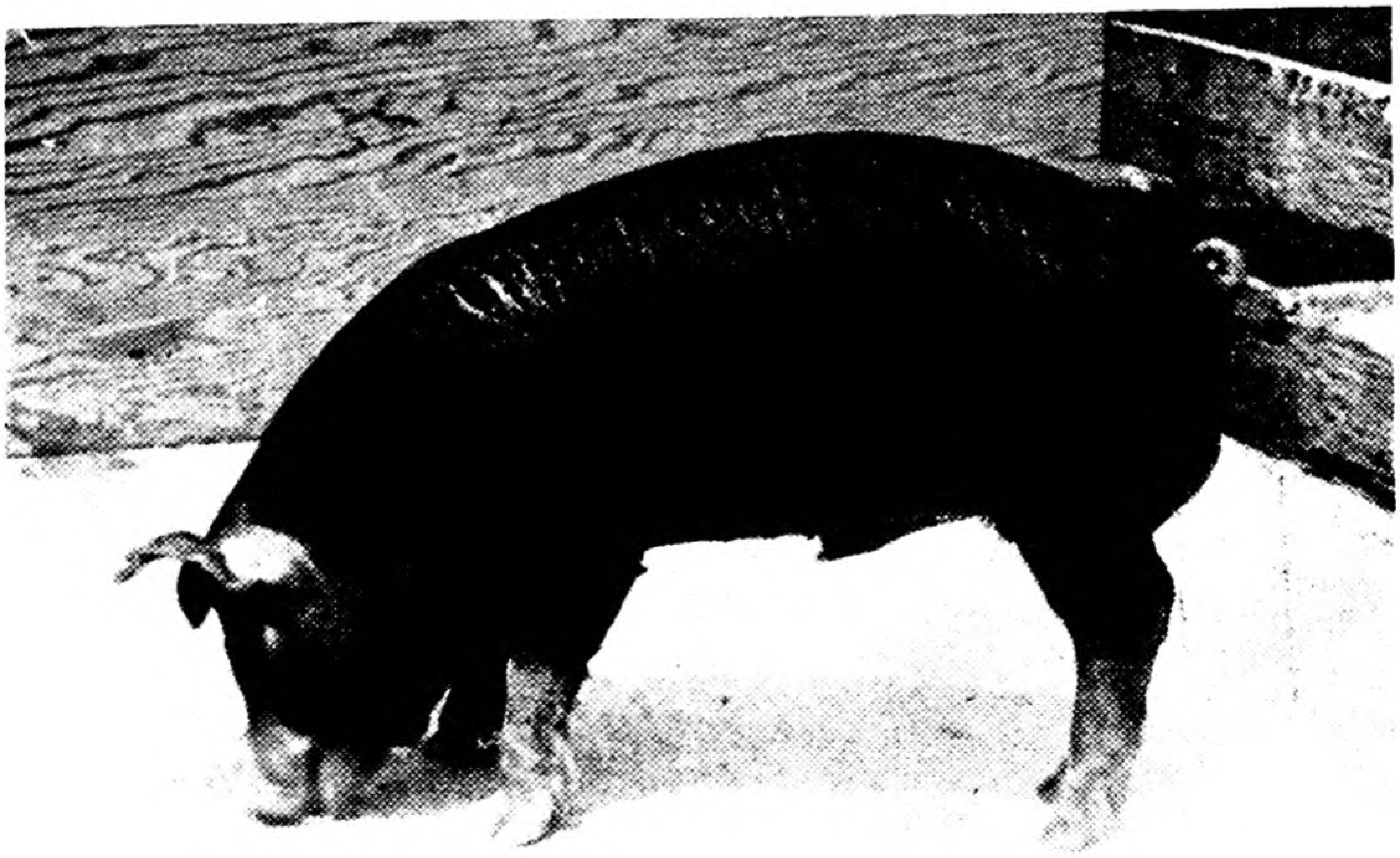


Pig No. 7

Figure 2.9. Two litter mates: pig No. 8 on tryptophan deficient diet lost 8 lb. in 21 days; pig No. 7 on the same diet plus 0·4% dl-tryptophan gained 25·5 lb. in 21 days. (By courtesy of Professor W. M. Beeson, Purdue University.)



Pig No. 2



Pig No. 1

Figure 2.10. Two litter mates: pig No. 2 on lysine deficient diet lost 2·0 lb. in 28 days; pig No. 1 on the same diet plus 2·0% dl-lysine-HCl gained 25·0 lb. in 28 days. (By courtesy of Professor W. M. Beeson, Purdue University.)

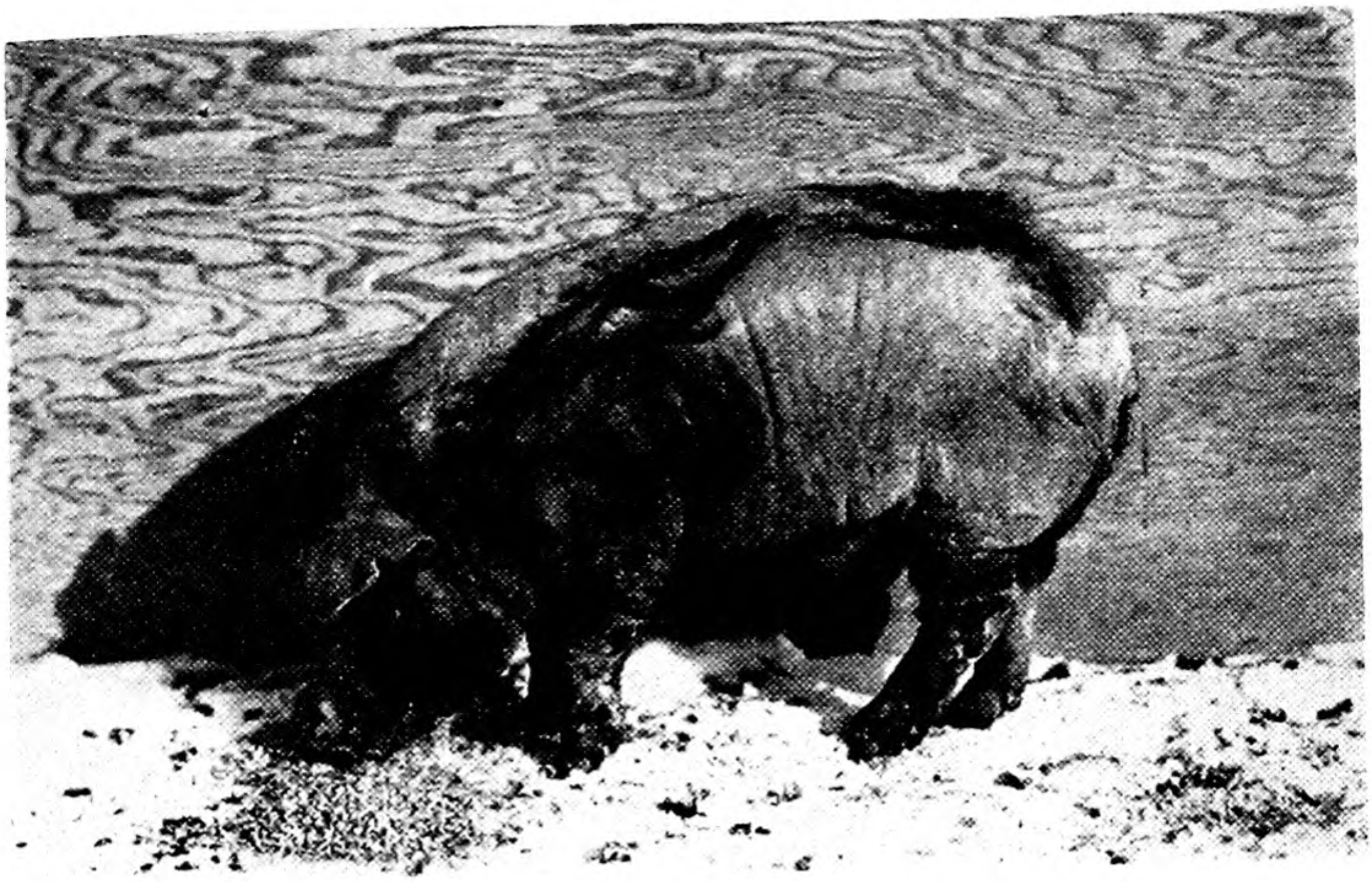
diet of pigs caused loss of weight and was responsible for decreased food consumption and efficiency of food utilization (*Figure 2.9*). Lack of lysine or valine in the diet resulted in cessation of growth and also affected adversely the food utilization (*Figure 2.10*). An acute deficiency of any one of the " essential " amino acids has the same effect as a lack of total protein. On the other hand, with an efficient balance of amino acids, the amount of protein required for growth may possibly be reduced below the standard values generally recommended. Thus, in future, the balance of the amino acid make-up of the diet rather than its total protein content may become the criterion for judging the quality of the ration.

It is recognized that proteins of animal origin are, on the whole, biologically superior to those derived from plants, and the old concept of first and second class protein was largely based on this distinction. When the emphasis shifted from the proteins to their component amino acids, it became evident that something more than the appropriate balance of these was responsible for the special virtue of animal protein. The property was attributed to the so-called animal protein factor, and considerable experimental effort was put into identifying this entity. Vitamin B_{12} has now been recognized as a component of the animal protein factor, but it is generally believed that some unidentified factors play a part in it as well. The addition of vitamin B_{12} to diets from purely vegetable sources has in many instances enhanced their value for pigs.

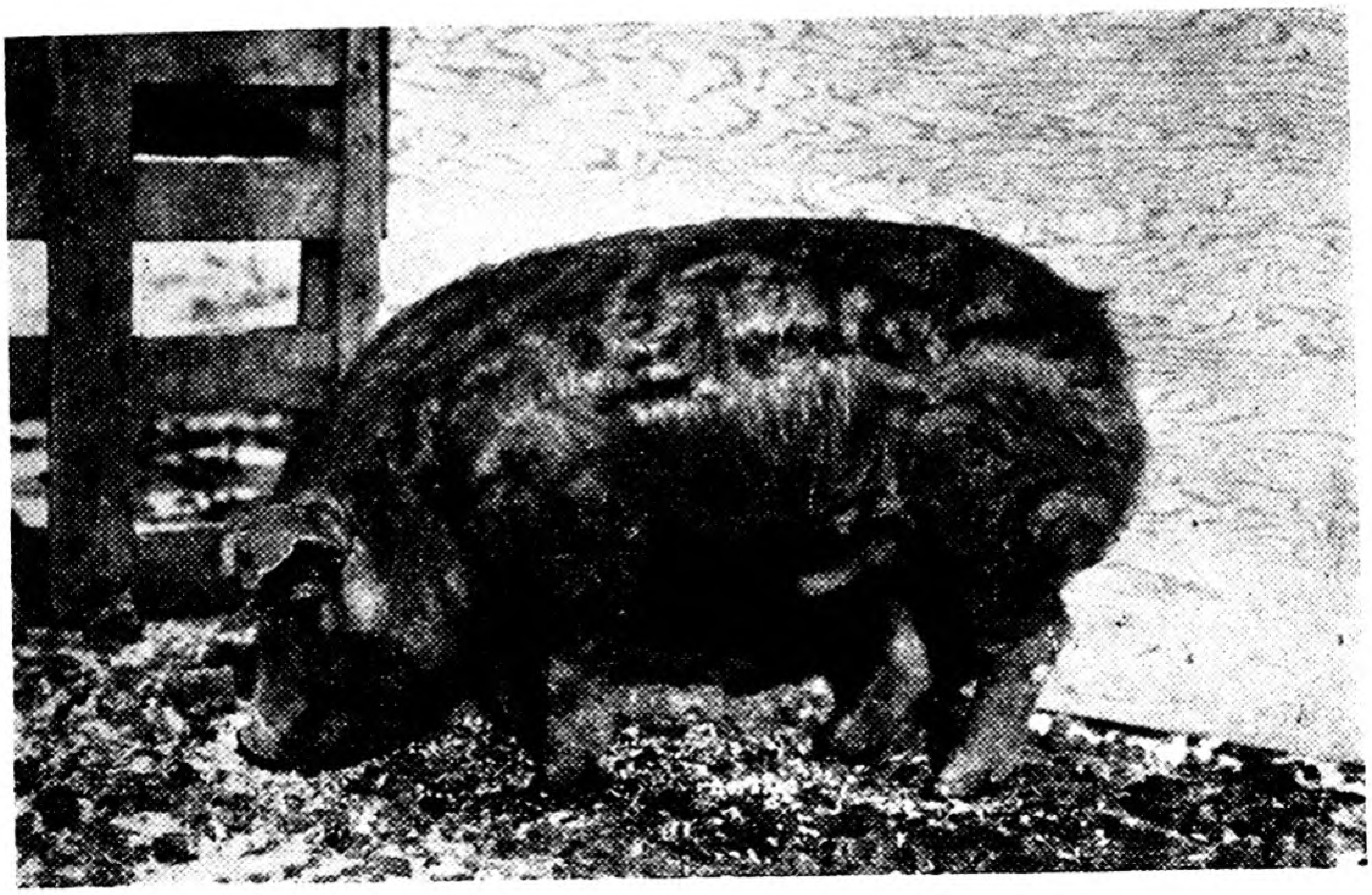
FAT

The fat requirement of the pig is a subject of great controversy. The pig can build fat from other nutrients, protein and carbohydrates. It has, however, been established that in spite of this ability a small amount of fat is essential for normal development, as a fat-free diet leads to deficiency signs. WITZ and BEESON (1951) demonstrated recently that as little as 0·12 per cent of fat was sufficient for normal development of young pigs, and only when the level was reduced to 0·06 per cent deficiency signs occurred—a scaly dandruff like dermatitis of the tail, back and shoulders, unthrifty appearance, loss of hair, a brown gummy exudate on the belly and sides, necrotic areas of the skin around the shoulders (*Figure 2.11*). Low-fat diets resulted in under-developed digestive system, small gall bladders and enlarged thyroids.

Apparently the pig cannot produce in its body some of the essential unsaturated fatty acids, such as the linoleic acid and arachidonic acid, which are required in fairly small amounts for the building of the cells and some of the organs in the body. Young growing animals must have these fatty acids provided in the diet, while adult animals, their growth completed, can do without them.



Pig No. 2



Pig No. 1

Figure 2.11. Two litter mates: No. 2—effect of a low fat-diet (0·06% ether extract). Note loss of hair, scaly dandruff-like dermatitis, especially on feet and tail; No. 1—receiving 5·0% of fat in diet. (By courtesy of Professor W. M. Beeson, Purdue University.)

The fat content of the fatty tissues increases markedly with the advancing age of the pig, and its chemical structure undergoes progressive changes. The fat becomes more saturated, and in consequence, its iodine number drops. Iodine numbers below 65 are associated with carcass fats of desirable characteristics. The faster the rate at which the fat is deposited in the fatty tissues, the more saturated the fat becomes. The bigger the proportion synthesized from carbohydrates, the higher the saturation of the deposited fat. According to CALLOW (1935) the fat synthesized from carbohydrates is relatively saturated with an iodine number of 50–60, whereas the fat formed from dietary fat is relatively unsaturated, with iodine number usually over 100. The higher the proportion of unsaturated fat, the less satisfactory the carcass fat, as it becomes more susceptible to oxidation and rancidity. This is the reason why the amount of dietary fat must be limited, and particular care must be taken to exclude fish oils, known to contain the highly unsaturated and unstable fatty acids. A most interesting observation was reported by CALLOW (1949), that pigs receiving a diet containing 23–31 per cent maize had fat unduly unsaturated and consequently soft, while those receiving a diet with 42–62 per cent maize showed the opposite characteristic. The author suggested that if the rate of deposition of fat is below a certain level, *e.g.* with the lower level of maize, the maize oil increases the degree of unsaturation in the deposited fat, while if the deposition of fat is above this level, *e.g.* with the higher level of maize feeding, the effect of the maize oil is masked by the deposition of more saturated fat.

FIBRE

There is experimental evidence available pointing to the fact that as the fibre content in the diet increases, the live weight gain and the efficiency of food utilization suffer. For example, ROBINSON (1930) has shown that by increasing the fibre content from 2·4 to 11·0 per cent, the daily gain of pigs was reduced from 1·25 lb. to 0·90 lb., and the amount of food required per unit of gain was increased by 62 per cent. The fibre content of a good quality meal for pigs should not exceed 5 per cent. Although it is known that the degree and manner of the utilization of the fibrous portion of feeds by pigs, and the digestibility of crude fibre may vary widely, little is known about the factors which influence the extent of its utilization. Direct observations on the degree to which the apparently digested fibre is utilized by the pig are few and contradictory (BREIREM, HUSBY and PRESTHEGGE, 1943; HOME, 1948; NORDFELDT, 1946; WOODMAN and EVANS, 1947). The most recent investigations, by NORDFELDT, SVANBERG and CLAESSON (1949) and FORBES and HAMILTON (1952), point to the advantage of substituting the crude fibre estimation in feeding stuffs with that of cellulose and lignin. Whilst cellulose is digested by the pig to a varying degree, 20–90 per cent, the lignin is digested only to 5 per cent. Apparently bacterial fermentation plays an important part in the digestion of cellulose by the pig.

WATER

Depending on age, up to four-fifths of the pig consists of water. Water plays a crucial part in the life of every cell in the body. It is an essential component of every body fluid, it is a carrier of nourishment, it acts as a solvent and an agent for important chemical reactions of digestion and metabolism, it assists in removing waste products and it often helps to control the body temperature. Table 2.24 taken from EVVARD (1929) gives the water requirement of the pig. It is evident that the requirement changes with age and that at any time it is to some extent related to environmental temperatures and humidity. The ratio of 3:1 is recommended for water and dry feed, particularly for young rapidly growing pigs. In fact, however, experimental evidence on optimum water intake of the various classes of pigs is very meagre. GARNER and SANDERS (1937) studied water consumption of nursing sows and found no correlation between prevailing temperatures and the amount of water drunk by the sows. The sows kept on pasture consumed daily 43 lb. of water, which, after making an allowance for the water in grass eaten by the sow, was equivalent to a total intake of about 53 lb. of water.

TABLE 2.24

THE WATER CONSUMPTION OF PIGS

(according to Evvard, 1929)

Weight of pig	*Water required for each pound dry matter consumed*	*Daily water consumption ad. lib. per pig*		*Weight of pig*	*Water required for each pound dry matter consumed*	*Daily water consumption ad. lib. per pig*	
		Spring pigs	*Autumn pigs*			*Spring pigs*	*Autumn pigs*
lb.	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*	*lb.*
25	2·62	3·3	2·5	200	1·35	9·0	9·6
50	2·35	5·5	4·5	225	1·23	8·5	8·5
75	2·40	8·5	7·0	250	1·03	7·5	7·5
100	2·04	9·0	7·5	275	0·94	6·5	7·0
125	1·85	9·5	8·5	300	0·86	6·0	6·0
150	1·67	10·0	9·0	350	0·72	5·3	5·3
175	1·72	11·5	10·5	400	0·69	5·2	5·2

VITAMINS

It is hardly possible to present in a tabular form the vitamin requirements of the pig. The nutritional requirement is a rather flexible quantity, particularly so when one has to take into account the possibility of synthesis within the body. It is quite possible for individuals to vary considerably in their requirements for vitamins, for various reasons, such as failure to digest or assimilate, increased tendency to excrete, or lack of ability to synthesize. The fact that, in recent years, definite interactions between different nutrients were established, complicated the matter still further. The existence of interrelationships between calcium, phosphorus and vitamin D, or tryptophan and nicotinic acid, for example, must lead to the conclusion that generalization in the field of vitamin requirements may be very misleading. In many instances, the results obtained in a specific investigation relate only to the particular set of circumstances in which the test was carried out, and one should be very careful in attaching a more general value to them. The fact that a considerable amount of the earlier work was done with analytical procedures which were not specific or sensitive, frequently resulting in conflicting evidence adds to the complexity. It is not surprising, therefore, to find a very great variation in results obtained by different workers investigating the requirement for a specific vitamin. Much confusion also resulted from the fact that different authors state their requirements in different terms. The fact that most of the investigations were carried out on weaner pigs also does not simplify the matter. The requirements of the baby pig and of the pregnant or lactating sow have, in very few instances only, been satisfactorily investigated, and most of the present-day recommendations referring to these classes of pig are either based on deductions from established requirements of a different age group, or empirical assumptions with no scientific evidence to support them. In these circumstances it may be helpful to assemble the data available in the literature for each of the vitamins separately, and present the requirement, first as stated by the author and then on a common basis, by calculating the amount which apparently would satisfy the requirements of either a 50 lb. or a 200 lb. pig. Averages were also calculated, and the National Research Council (1950) recommendations are given for comparison in each case. Whenever available, the requirements of baby pigs and breeding stock are also stated. Further, a very brief description of the signs associated with a deficiency of a vitamin is also given, with general observations which may be of significance. It must be stressed, however, that a single specific sign of deficiency is very rare, and more often than not secondary signs mar the picture, frequently reducing it to general signs descriptive of a " badly doing " pig.

FAT SOLUBLE VITAMINS

Vitamin A.—Table 2.25 summarizes the available evidence on vitamin A and carotene requirements. It is important to remember that vitamin A, as such, does not occur in plants, which contain the

Table 2.25

CAROTENE AND VITAMIN A REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
		µg.	µg.
Carotene			
Dunlop (1934)	14–62 mg./100 lb. diet	350–1,550	910–4,030
Dunlop (1935)	90·3 mg./100 lb. diet	2,258	5,870
Guilbert *et al* (1937)	25–39 µg./kg. body weight	568–886	2,273–3,545
Hale and Fraps (1940)	100µg./100 g. diet	1,117	2,954
Braude *et al* (1941)	30 i.u./lb. body weight	900	3,600
Hentges *et al* (1952)	25µg./kg. body weight	568	2,273
Average		1,086	3,379
National Research Council (1950)		2,000	8,000
National Research Council (1950)	Pregnant females 18–23 mg./day Lactating females 32·5–37·5 mg./day		
Vitamin A			
Mollgaard (1938)	2,500 i.µ./day	758	758
Guilbert *et al* (1940)	4·4–5·7 µg./kg. body weight	100–130	400–518
Braude *et al* (1941)	10 i.u./lb. body weight	167	667
Average		347	628

precursors of the vitamin : carotene and cryptoxanthin. The pig can utilize these precursors, and it is known that they are converted into vitamin A in the small intestines of the pig (Thompson *et al*, 1950). The efficiency of conversion depends on a number of factors. The utilization of carotene by the pig is about three times less effective than of true vitamin A, and thus, on weight basis, about three times as much carotene as vitamin A should be supplied to cover the requirement of the pig. Until recently, the only commercial supplement of vitamin A for feeding to pigs was fish oil, notably cod liver oil. It was generally appreciated that the stability of vitamin A in a mixed ration containing cod liver oil was not good, and thus, a wide margin of safety was allowed. Recent developments point to the use of synthetic preparations of vitamin A in the form of a powder, in which each particle of the vitamin is protected by a micro-crystalline wax. In the future, cod liver oil will in all probability be completely replaced by such a product.

Vitamin A is essential for growth and reproduction. Deficiency manifests itself in retardation of growth, lack of appetite, nervous disorders associated with nerve degeneration, a tendency to carry the head tilted to one side, incoordination of walk, spasticity with gradually increasing convulsive fits, paralysis, xerophthalmia and other eye abnormalities, failure to breed or production of dead or non-viable offspring, with malformations of many types (*Figure 2.12*).

Vitamin D.—In Table 2.26 the evidence on the requirement of pigs for vitamin D is tabulated. In considering the vitamin D requirement, its relation to calcium and phosphorus must be remembered.

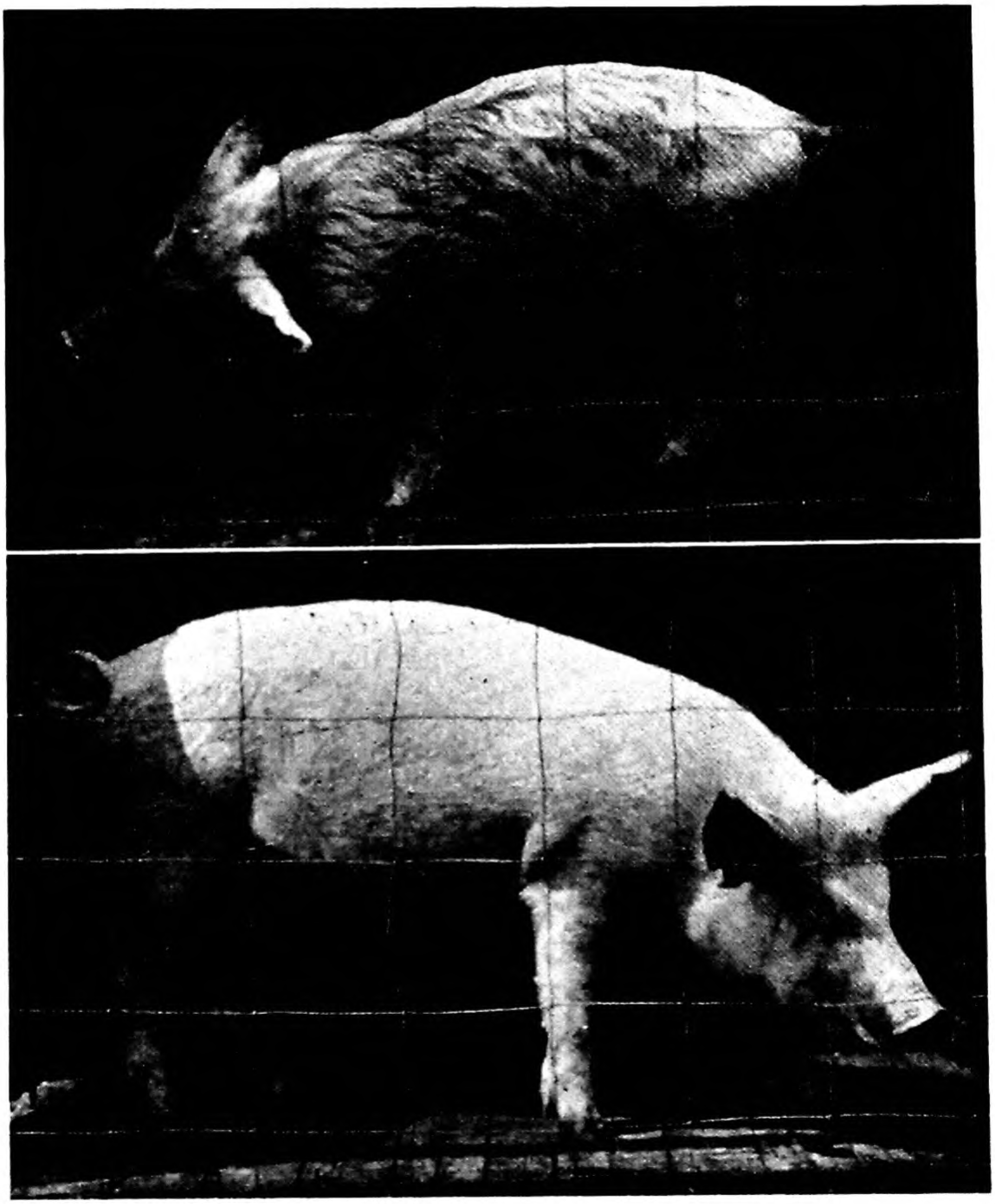


Figure 2.12. Above—a pig after 162 days on vitamin A deficient diet. Below—the same pig 2 months later after receiving a large single dose of vitamin A.

TABLE 2.26

VITAMIN D REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
Johnson and Palmer (1941)	200–250 i.u./day on rations containing 1·07% Ca and 0·65% P	200–250 i.u.	
Bethke *et al* (1946)	90 i.u./lb. diet containing 0·6% Ca. 0·45% P	225 i.u.	585 i.u.
Ohio Agric. Exp. Sta. (1944)	10–20 i.u./100 g. diet	117–234 i.u.	295–590 i.u.
Average		208 i.u.	419 i.u.
National Research Council (1950)		150 i.u.	375 i.u.
National Research Council (1950)	Pregnant sows, 300–375 i.u. Lactating sows, 550–625 i.u.		

Vitamin D may be obtained by the animal from solar irradiation of the 7-dehydrocholestrol present in their skin. Recently, ABRAMS (1952) has calculated that, under average farm conditions in Britain, the vitamin D produced by the solar irradiation is just about equal to, or more probably less than, the amounts which the animal needs for normal health and reproductive functions. Using his figures, one can calculate that on the average, a pig with 1,000 sq. cm. of skin surface for irradiation would derive from sunshine 375–560 i.u. of vitamin D daily. It follows then that growing pigs kept all the year out of doors need not receive a vitamin D supplement, whilst the necessity to provide the latter for pigs kept indoors and gestating or lactating sows is obvious. One should also keep in mind the fairly frequent adverse climatic conditions prevailing in Britain, which may be responsible for a considerable reduction in the amounts of vitamin D derived from solar irradiation of the skin.

There are two forms of vitamin D used in supplementing rations for livestock, D_2 and D_3, and the pig can apparently utilize both. The D_2 is usually produced by irradiation of ergosterol, while D_3 by irradiation of the animal sterol, 7-dehydrocholesterol. Cod liver oil has been widely used as a source of vitamin D for pigs. Recently a synthetic product has been made available, at a reasonable price.

The vitamin D plays a part in the absorption of calcium and phosphorus from the intestinal tract, and to some extent it also controls skeletal development. Deficiency of vitamin D causes rickets, particularly in the young animal. Failure to grow, enlarged joints, stilted gait, paralysis, rough hair coat and broken bones are the usual signs. In advanced stages, the blood-serum calcium is lowered to 6 mg. or less per 100 ml. (normal: 10–12 mg.). The blood phosphorus may be also lowered.

Vitamin E.—Although it is known that vitamin E (alpha tocopherol) is required by the pig, its specific functions have not been fully established as yet. It has been suggested that vitamin E acts primarily through some enzyme systems, and accordingly, in a non-specific manner, as a physiological anti-oxidant. Under practical feeding conditions, a vitamin E deficiency has not been reported in pigs. The term ' reproductive vitamin ', as vitamin E is sometimes referred to, finds little support in relation to pigs. Feeding a vitamin E deficient diet to sows may result in a lower reproductive performance, due to the death of embryos rather than to any interference with ovulation and implantation. Pigs from sows fed a vitamin E deficient diet exhibited stiffness of gait, convulsions and muscular incoordination caused by disintegration and necrosis of the muscle fibres. Severe vitamin E deficiency leads to a form of muscular dystrophy, characterized by a gradual replacement of normal muscle fibres with fibrous tissue. In both the skeletal and cardiac musculature, hyaline degeneration has been observed, and under some conditions, abnormalities of the fatty depots were noticed. The role of vitamin E as a natural anti-oxidant is of some importance, as the deterioration of the fat tissues of slaughtered animals during cold storage is a problem in the pig industry. It has been demonstrated that pigs receiving a diet low in vitamin E and rich in cod liver oil developed after slaughter a deep-yellow colour of the back fat. Fish liver oils, and more particularly the unsaturated fatty acids contained in them possess an anti-vitamin E activity.

At this stage, it is unwise to recommend specific values for vitamin E requirements of pigs, as even a minimum estimate may be grossly in error, when the other constituents of the ration are taken into account.

Vitamin K.—Hardly anything is known about this vitamin in relation to pigs. Under experimental conditions, the chief defect associated with vitamin K deficiency is the failure of the blood to clot on standing, this being due to the fact that the absence of vitamin K prevents the formation of prothrombin. Under practical conditions, no deficiency state has yet been reported.

WATER SOLUBLE VITAMINS

Thiamine—vitamin B_1.—The requirement of the pig for aneurin (or thiamine as it is now called) is summarized in Table 2.27.

Thiamine deficiency manifests itself in a reduced appetite, vomiting, impairment of respiration, diarrhoea, disturbances of movement and of circulation and cardiac disorders. The cardiac disorders are rather specific (*Figure 2.13*) and on post-mortem examination, an excess of pericardial fluid and dilation of the auricle and ventricle are found. Necrosis and fibrosis of the myocardium, and other degenerative changes have also been reported.

TABLE 2.27

THIAMINE REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
		µg.	µg.
Hughes (1940b)	1 mg./100 lb. body weight	500	2,000
Van Etten *et al* (1940)	25–37 µg./kg. body weight	568–840	2,273–3,363
Ellis and Madsen (1944)	47 µg./kg. body weight	1,067	4,272
Heinemann *et al* (1946)	0·19–0·21 mg./kg. body weight	4,319–4,773	17,271–19,089
Hatzler (1949)	900 µg./lb. diet	2,250	5,850
Jacobsen *et al* (1950)	45–75 µg./kg. body weight	1,024–1,703	4,190–6,818
Ferrando (1952)	1·5–1·8 µg./kg. diet	1,755–2,106	4,950–5,940
Average		1,766	6,296
National Research Council (1950)		1,500	3,800
National Research Council (1950)	Pregnant females 3·0–3·8 mg./day Lactating females 5·5–6·3 mg./day		

Thiamine is involved in tissue oxidation of carbohydrates, particularly in reactions involving decarboxylation of pyruvic acid. The principal biochemical features of deficiency are : an increased blood and urinary pyruvate and lactate and decreased thiamine and cocarboxylase. It is interesting to note that in some recent studies the observed appetite failure in pigs subjected to sub-optimum intake of thiamine was preceded by marked elevation of blood pyruvate.

Riboflavin.—The evidence on the riboflavin requirements of pigs is summarized in Table 2.28. It is interesting to note that recently

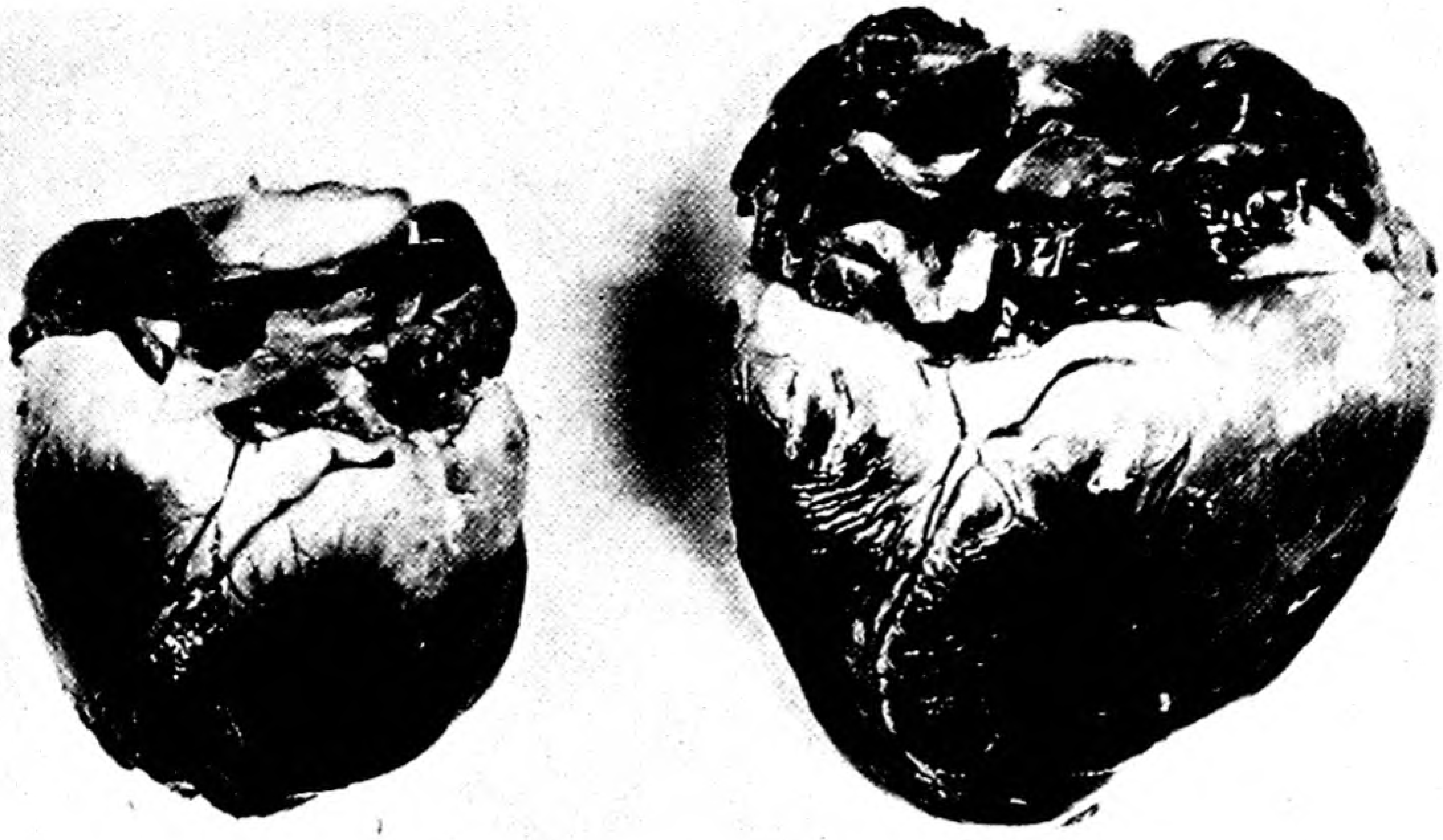


Figure 2.13. The heart on the left is from a pig fed a purified ration with adequate thiamine. The heart on the right is that of a pig fed the same ration without thiamine. Live weights of the two pigs were 89 lb. and 65 lb., and heart weights 8·3 oz. and 11·0 oz. respectively. (By courtesy of Professor T. J. Cunha, University of Florida).

MITCHELL *et al* (1950), reported the effect of a change in environmental temperature on the riboflavin requirement of growing pigs. They found that at 85°F the requirement was about 1·2 p.p.m. of air dry feed, while that at 42°F was about 2·3 p.p.m.

The signs of riboflavin deficiency are: poor appetite, retarded growth, rough hair coat and skin, sometimes caked with sebaceous exudate, secretions around the eyes, swollen eyelids, development of lens cataract, anorexia, vomiting, inability to stand normally. Slow and irregular pulse and respiration, cyanosis and drop in body temperature are also often encountered.

Post mortem signs include: thickened skin, oedematous areas beneath the skin, oedematous fluid infiltrated between muscles, under muscular sheath and in the abdominal and thoracic cavities, enlarged spleen, anaemia, light grey discoloration of kidneys.

Riboflavin, by reason of its participation in enzyme systems involved in carbohydrate, protein and purine metabolism, facilitates the liberation of food energy and assimilation of food nutrients, thus having a direct effect on the economy of food utilization.

Nicotinic acid.—Evidence is now available that in the pig, as in most animals, tryptophan can supplant nicotinic acid, and thus prevent the signs associated with the deficiency of this vitamin. Most of the values given in Table 2.29 as nicotinic acid requirements of pigs have been obtained before the nicotinic acid–tryptophan relationship was established, and thus these values have only a limited application.

TABLE 2.28

RIBOFLAVIN REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
		mg.	*mg.*
Hughes (1940a)	1–3 mg./100 lb. body weight	0·5–1·5	2·0–6·0
Krider *et al* (1949)	1·4 mg./lb. diet	3·5	9·1
McMillen *et al* (1949)	2·5 mg./lb. diet	6·3	16·3
Mitchell *et al* (1950)	0·55 mg./lb. diet at 85°F	1·4	3·6
	1·59 mg./lb. diet at 42°F	4·0	10·3
Miller and Ellis (1951)	0·83 mg./lb. diet	2·1	5·4
Carpenter (1952)	2·5 mg./kg. diet	2·9	7·4
Ferrando (1952)	1·6 mg./kg. diet	1·9	5·3
Moustgaard (1952)	1·3 mg./kg. diet	1·5	4·3
Average		2·7	7·3
National Research Council (1950)		2·5	6·3
Forbes and Haines (1952)	Baby pigs—1·5–2·0 mg./kg. dry matter	—	—
Lehrer and Wiese (1952)	Baby pigs—1·0–1·5 mg./day	—	—
Stevenson *et al* (1952)	Pregnant and lactating sows 1·25 mg./lb. diet	—	—
National Research Council (1950)	Pregnant sows, 5·0–6·3 mg./day Lactating sows, 9·2–10·5 mg./day		

They are valid only for the dietary regime under which the experiments were carried out. The fact that administration of tryptophan to the pig results in the excretion of increased amounts of nicotinic acid metabolites in the urine supports the idea that tryptophan is converted into nicotinic acid in the body.

Signs of nicotinic acid deficiency include: anorexia, slowed growth, a rough scruffy skin, colitis and a high incidence of diarrhoea, necrotic colon and caecum.

Pantothenic acid.—Table 2.30 summarizes the evidence on requirements for pantothenic acid. Pantothenic acid deficiency signs include: decreased rate of gain, inefficient utilization of food, loss of hair, reddening and scaliness of the skin, colitis accompanied by severe diarrhoea, locomotor incoordination, spastic gait, "goose stepping" (*Figure 2.14*), alopecia, excessive nasal secretion and normocytic anaemia. On autopsy, degenerative changes and haemorrhages in liver, kidneys and intestines, atrophy of glandular tissue in the stomach and in the

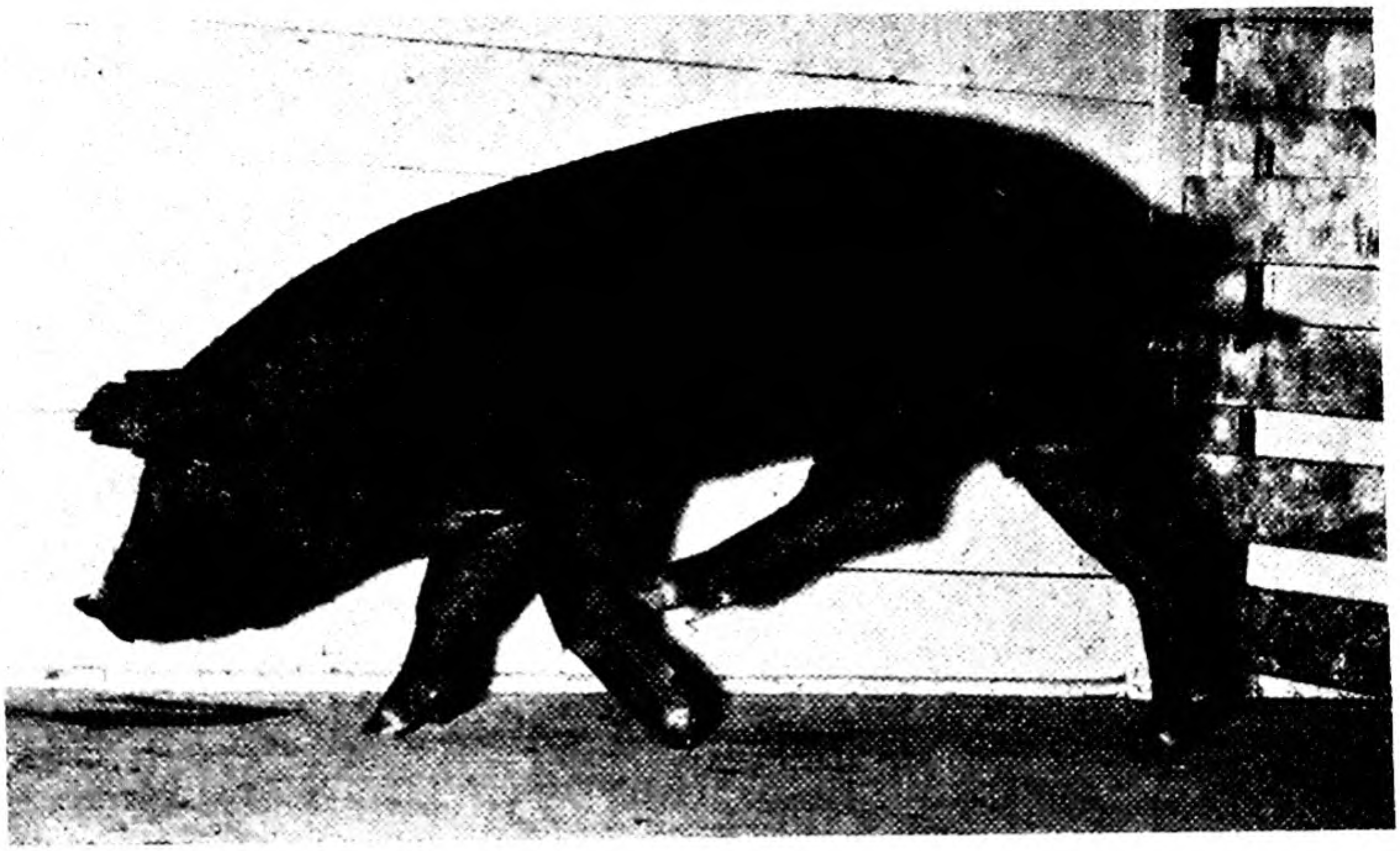


Figure 2.14. "Goose stepping"—a sign of pantothenic deficiency. (By courtesy of Professor R. W. Luecke, Michigan State College.)

TABLE 2.29

NICOTINIC ACID REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
		mg.	*mg.*
Hughes (1943)	5–10 mg./100 lb. body weight	2·5–5·0	10–20
McMillen *et al* (1945)	15–25 mg./lb. diet	37·5–62·5	97·5–162·5
Braude *et al* (1946)	5–10 mg. daily	5–10	5–10
Powick *et al* (1947)	0·7–0·8 mg./kg. body weight	16–18	63–73
Luecke *et al* (1948)	17·4 mg./day, not quite enough	17·4	17·4
Burroughs *et al* (1950)	0·65 mg./kg. body weight	14·8	59
Ferrando (1952)	5 mg./kg. diet	5·9	14·8
Moustgaard (1952)	5 mg./kg. diet	5·9	14·8
Average		15·3	40·8
National Research Council (1950)		15	38
Powick *et al* (1947b)	Baby pigs: 0·6–1·0 mg./kg. body weight		
National Research Council (1950)	Pregnant females 30–38 mg./day		
	Lactating females 55–63 mg./day		

Table 2.30

PANTOTHENIC ACID REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
		mg.	*mg.*
Hughes and Ittner (1942)	250 µg./kg. body weight	5·7	22·7
McMillen *et al* (1949)	10 mg./lb. diet	25·0	65·0
Emsbo *et al* (1949)	250 µg./kg. l.w. not sufficient	5·7	22·7
Luecke *et al* (1949)	15 mg./lb. diet	37·5	97·5
Wiese *et al* (1951)	10–20 mg./lb. diet	25–50	65–130
Benninson *et al* (1951)	3·7 mg./lb. diet	9·3	24·0
Sharma *et al* (1952)	10 mg./lb. diet	25·0	65·0
Owen and Bowland (1952)	2·5 mg./lb. diet	6·3	16·2
Carpenter (1952)	10–12 mg./kg. diet	11·8–14·2	29·5–35·4
Moustgaard (1952)	10 mg./kg. diet	11·8	29·5
Luecke *et al* (1952)	5–9 mg./lb. diet	12·5–22·5	32·5–58·5
Average		17·7	47
National Research Council (1950)		14	35
Strothers *et al* (1952)	Baby pigs—1–2 mg./100 g. solids in milk substitutes		

intestines have been observed. It has been suggested that there is a relationship between the protein and the pantothenic acid requirements. It has been reported recently that nitrogen retention appears to be impaired on rations deficient in pantothenic acid, and that a high level of protein in the diet exercises a sparing effect on the pantothenic acid requirement of pigs.

Pyridoxin.—Table 2.31 summarizes the evidence on pyridoxin requirements of pigs. The signs of pyridoxin deficiency are : poor appetite, reduced growth, unsteady gait, locomotor disturbances in the hind legs, epileptic fits and convulsions, coma, rough hair coat, brown exudate around the eyes and microcytic hypochromic anaemia. Post-mortem signs include : fatty infiltration of the liver, lesions in the nervous system and some degenerative changes in the muscles.

Pyridoxin is now known to be active in enzymic systems involved in protein metabolism. Deficiency of pyridoxin causes considerable disturbance of the amino acid metabolism and protein synthesis. The formation of haemoglobin and certain serum proteins may be impaired through lack of pyridoxin. It has been suggested recently that the formation of euglobulins, the fraction of blood which carries

TABLE 2.31

PYRIDOXIN REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
		mg.	*mg.*
Hughes and Squibb (1942)	Up to 5 mg./100 lb. body weight	2·5	10·0
Wintrobe *et al* (1943)	40 µg./kg. body weight	0·9	3·6
McMillen *et al* (1949)	2·5 mg./lb. diet	6·2	16·2
Moustgaard *et al* (1952)	40–50 µg./kg. body weight to prevent deficiency	0·9–1·1	3·4–4·5
	80–100 µg./kg. body weight for optimum protein utilization	1·8–2·3	7·2–9·0
Average		2·6	8·4
National Research Council (1950)		1·8	—
Lehrer *et al* (1951)	Baby pigs—0·65 mg./kg. liquid diet	—	—

the antibodies, may be adversely affected by deficiency of pyridoxin.

Vitamin B_{12}.—Vitamin B_{12}—cyanocobalamin is the latest addition to the list of vitamins. It was discovered in 1948, and is now known to play an important part in the utilization of protein by the normal pig. It forms a part of what was formerly described as the Animal Protein Factor, and is to a high degree responsible for the recognized nutritional difference between proteins of animal and vegetable origin. Vitamin B_{12} contains cobalt in its molecule, and, as such, is the only vitamin, known at present, associated directly with a metal.

Evidence is now available that vitamin B_{12}, or vitamin B_{12}-like substances, can be synthesized in the digestive tract, probably in the lower part of the small intestines.

Table 2.32 summarizes the evidence on the requirements of pigs for vitamin B_{12}. The recorded deficiency signs include : persistent loss of appetite, hyperirritability, an exudate with local skin lesions, emaciation, posterior incoordination and normocytic anaemia (*Figure 2.14*). On post mortem, liver damage, necrosis of the cells and fatty infiltration is usually encountered. Sows fed deficient rations produced fewer piglets and piglets with low vitality. The sows, themselves, do not exhibit any clinical signs of deficiency, but their offspring is adversely affected.

TABLE 2.32

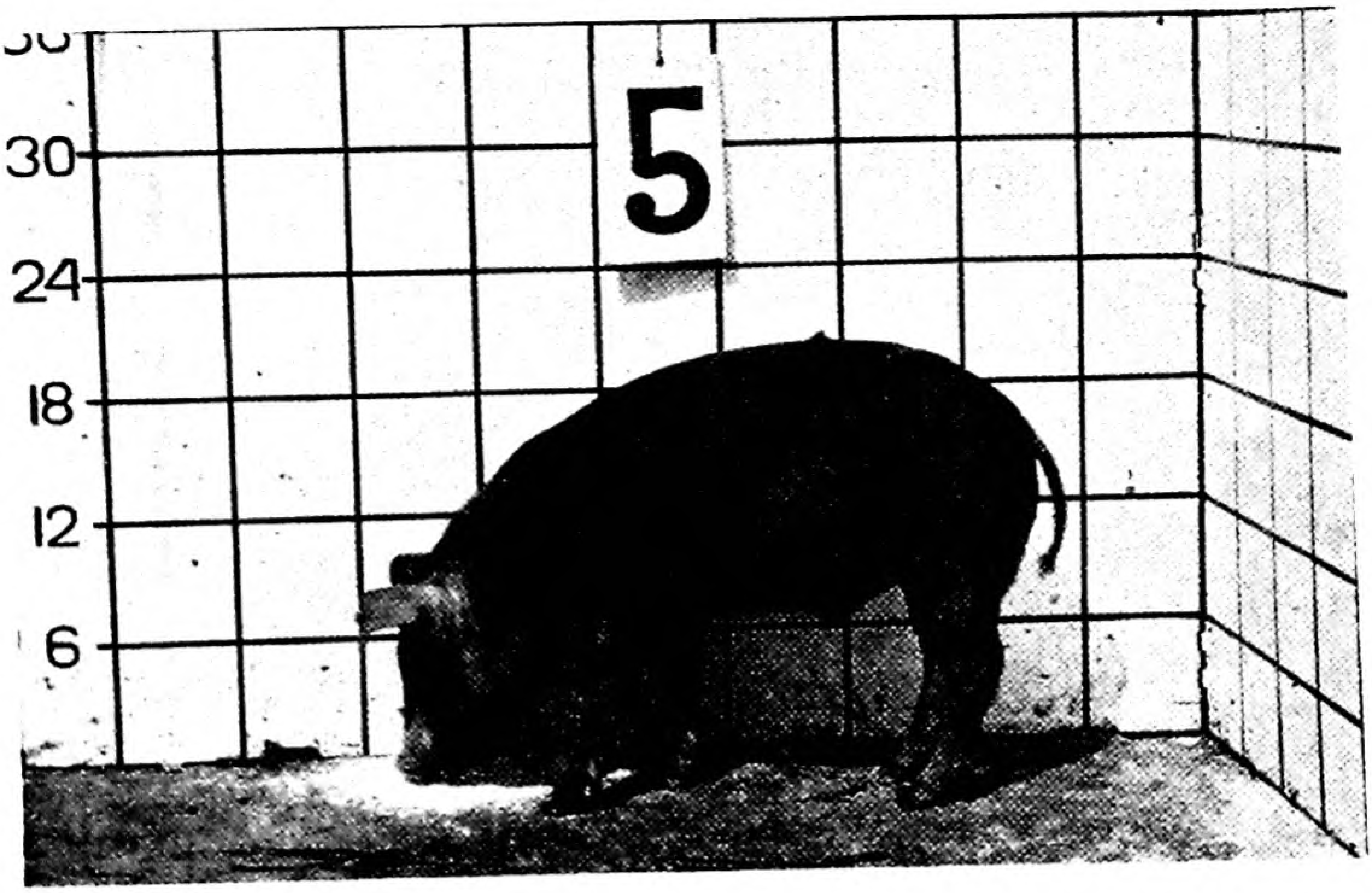
VITAMIN B_{12} REQUIREMENTS

Reference	*As stated by the investigators*	*Calculated daily requirement of a pig weighing*	
		50 lb.	*200 lb.*
		μg.	μg.
Catron and Culbertson (1949)	5–10 μg./lb. diet	12·5–25·0	32·5–65·0
Vohs *et al* (1951)	5 μg./lb. diet	12·5	32·5
Richardson *et al* (1951)	5 μg./lb. diet up to 75 lb.	12·5	—
Catron *et al* (1952)	4 μg./lb. diet up to 100 lb.	10·0	—
Average		13·4	40·6
National Research Council (1950)		—	—
Neuman *et al* (1950)	Baby pigs—50 μg./kg. dry matter of milk substitute		
Anderson and Hogan (1950b)	Baby pigs—0·26 μg./kg. live weight		
Nesheim *et al* (1950)	Baby pigs—20 μg./kg. dry matter, or 0·6 μg./kg. body weight daily by injection		

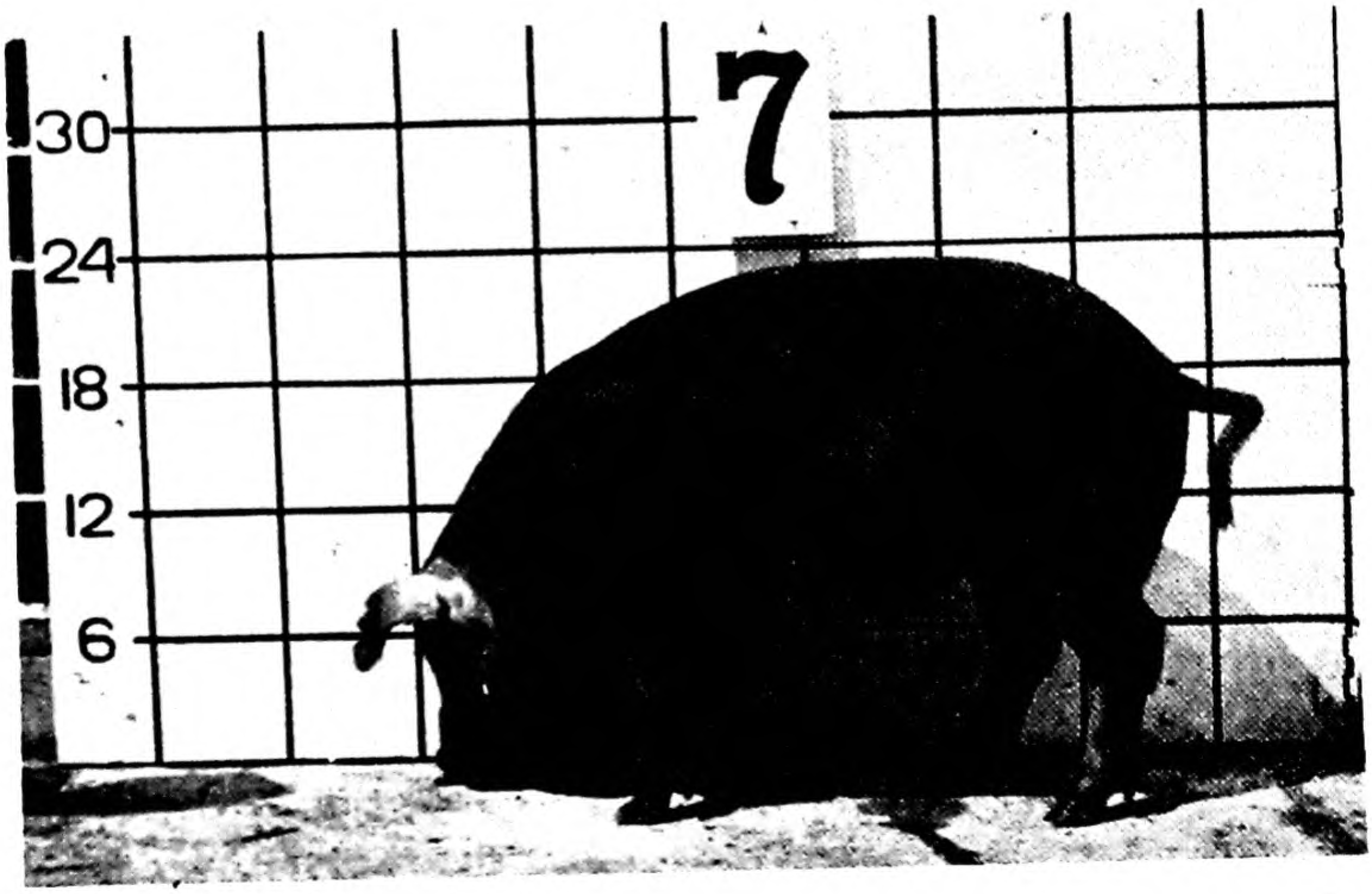
Inositol.—Inositol has been shown to be necessary to pigs receiving a synthetic diet under laboratory conditions. Under practical conditions, a deficiency of this vitamin is unlikely, as it is widely distributed in natural components of a pig's diet. Supplementation of a practical diet with inositol has no effect whatsoever.

Folic acid (*Pteroyl glutamic acid*).—Under practical conditions, a deficiency of folic acid is unlikely to occur in pigs. Under experimental conditions, a deficiency can be established by the use of a folic acid antagonist. The signs of this deficiency are: poor appetite, hair loss, diarrhoea, normocytic anaemia. The animals become listless and weak.

Choline.—The requirement of pigs for choline has been demonstrated, and deficiency signs, ascribed to lack of it in the diet, are: poor growth, lack of proper rigidity in the joints, particularly shoulders, reproductive failure and fatty liver (*Figure 2.16*). The picture is complicated, however, by the established interrelationship between choline, methionine and betaine. They all function as "methyl" donors in the body, and as such, can, to a great extent, replace each



Pig No. 5



Pig No. 7

Figure 2.15. Vitamin B_{12} deficiency in the pig—pig 5 received no vitamin B_{12} while its litter mate, pig 7, was fed the same ration, but including vitamin B_{12}. (By courtesy of Prof. D. V. Catron, Iowa Agr. Exp. Station.)

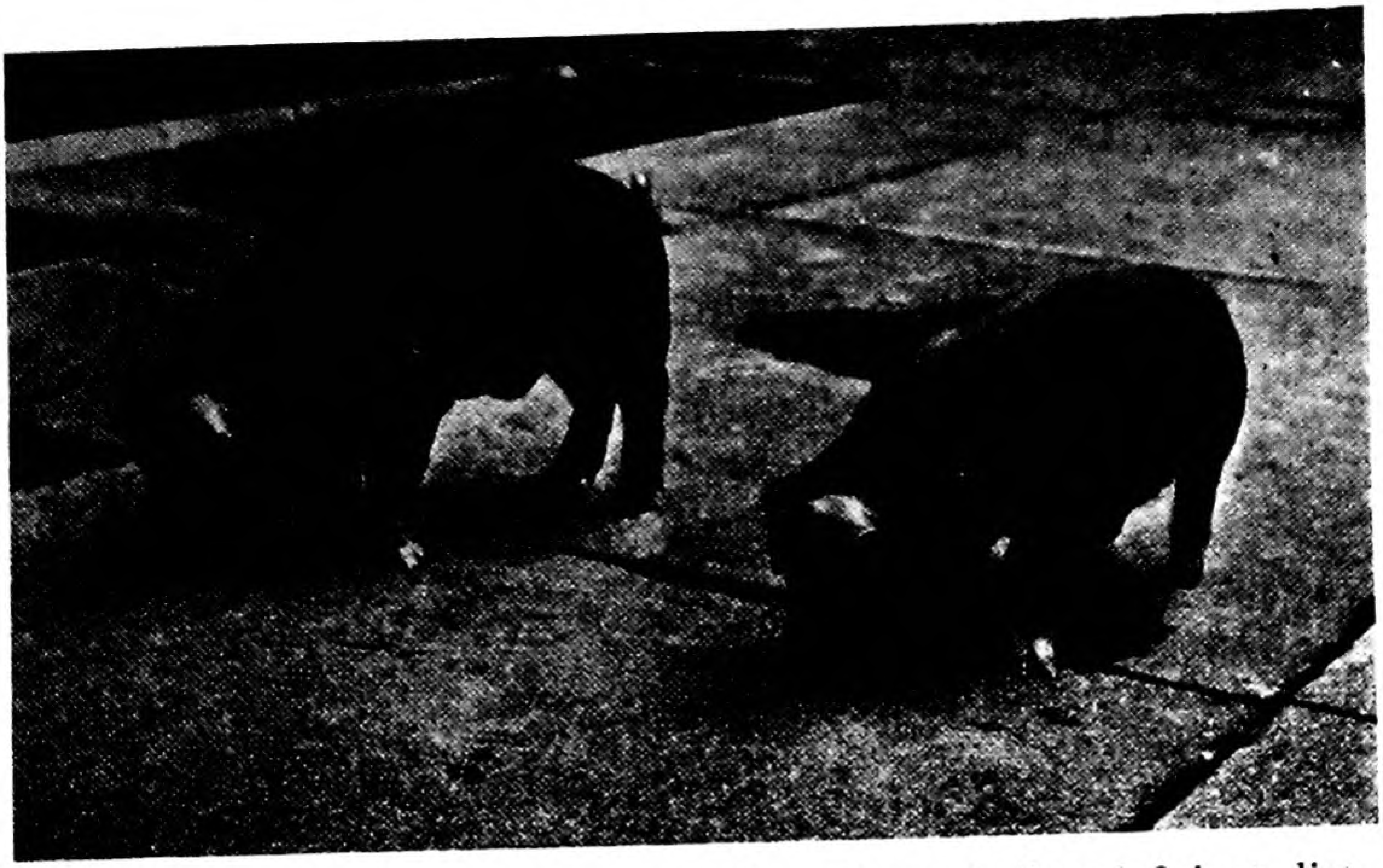


Figure 2.16. Two litter mates: normal and on choline deficient diet. (By courtesy of Professor B. C. Johnson, University of Illinois.)

other. However, it is quite possible that choline may have some other specific function in the body. Apparently, young pigs require about 450 mg. of choline per lb. of feed.

Biotin.—Biotin deficiency is unlikely to occur under practical conditions, as it is widely distributed in common feeds, and is also synthesized in the intestinal tract of the pig. Experimentally produced deficiency signs in baby pigs include: dermatitis, alopecia, skin ulceration, brown eye exudate, diarrhoea, transverse cracking and bleeding of the feet (*Figure 2.17*) and inflammation of the mucous membrane of the mouth. Deficiency symptoms can be prevented by 0·01 mg. of biotin per pig per day.

Vitamin C.—Experimental attempts to produce scurvy in pigs have failed. The pig can dispense with vitamin C in its food. BRAUDE, KON and PORTER (1950), who studied the vitamin C metabolism of the pig, produced evidence that the piglet is able from birth to synthesize vitamin C.

MINERALS

The mineral requirements of pigs have been investigated to a very limited extent only. This field has been very much neglected in recent years, and most of the fundamental evidence available is a decade or more old.

WIDDOWSON (1950) has analysed the composition of a newly born pig and reported the following amounts of minerals per kg. body weight on fat-free basis (the percentage of fat in the body was 1·1%): Ca—9·99 g., P—5·75 g., Na—2·41 g., K—2·09 g., Mg—0·32 g., Fe—0·029 g., Zn—0·01 g.

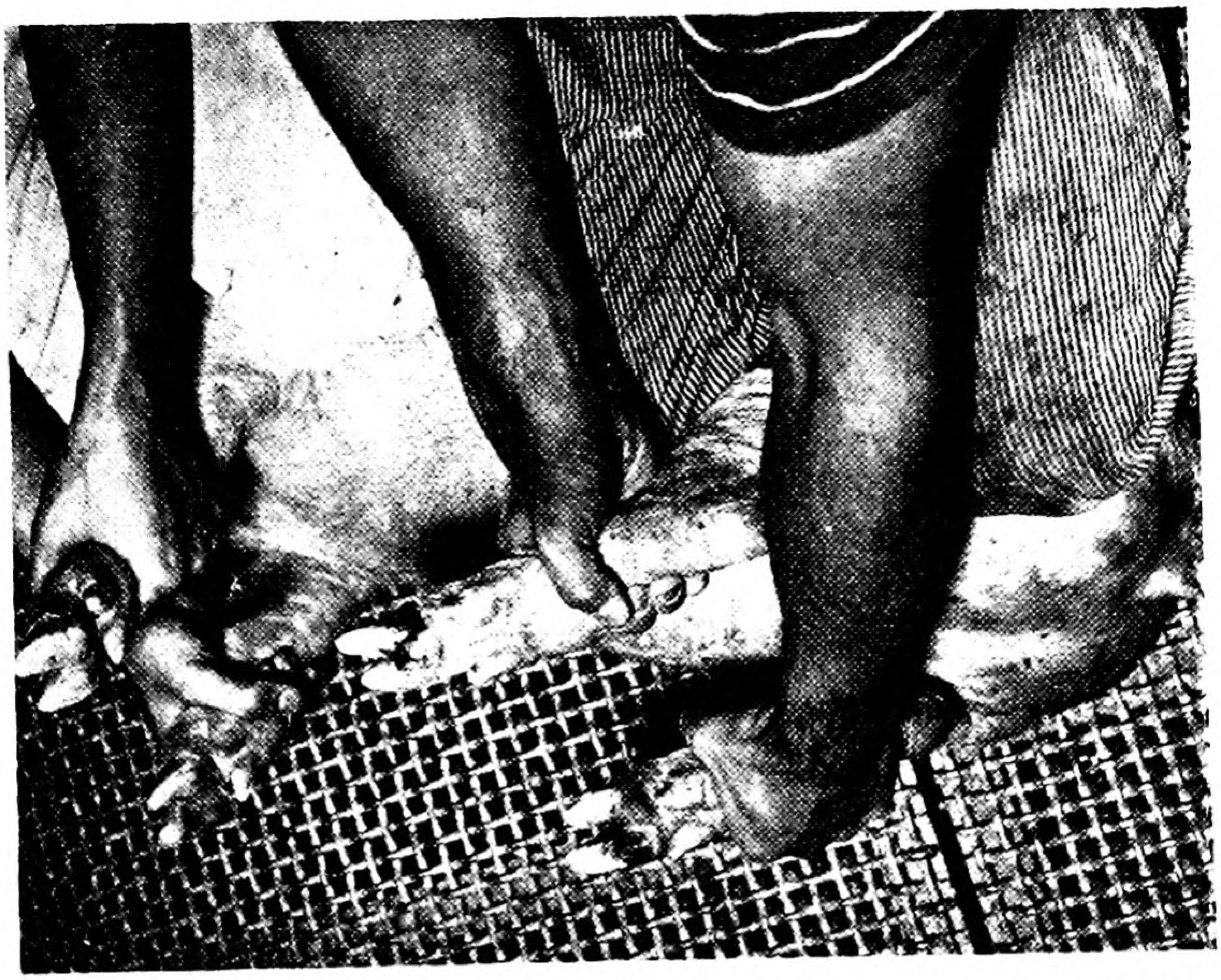


Figure 2.17. Characteristic cracks in the feet of pigs fed a diet deficient in biotin. (By courtesy of Professor T. J. Cunha, University of Florida.)

According to KAEGI (1935) a pig receiving a well-balanced diet on the average puts down the following amounts of major minerals per kg. live weight increase: Ca—7·95 g., P—7·05 g., S—4·68 g., Cl—1·97 g., Mg—2·21 g., K—1·32 g., Na—1·21 g. Obviously, the diet must provide these amounts of the minerals and also cover additional requirements of gestation and lactation.

The amount of an element in an animal must not be considered a criterion of its relative value, for some elements present in very small quantities are as essential as those which compose the greater portion of the animal.

The two most important minerals in pig nutrition are: calcium and phosphorus. Calcium forms about 1·5 per cent of the body, and phosphorus about 1 per cent. About 99 per cent of the former, and 75–85 per cent of the latter, is in bone and teeth. The functions of phosphorus in the body also include its participation in the metabolism of carbohydrates, fats and proteins. Table 2.33 gives the requirements of pigs for these two minerals. The balance between them is of the greatest importance and thus the Ca:P ratio should never be neglected when composing rations for the pig. It is also of great importance to keep in mind that the animal can, in cases of temporary deficiency in the ration, mobilize its calcium reserves, while there is no mechanism available for mobilizing phosphorus.

TABLE 2.33

CALCIUM AND PHOSPHORUS REQUIREMENTS OF GROWING AND FATTENING PIGS AND OF PREGNANT SOWS (400 LB.) EXPRESSED AS PERCENTAGES OF THE DRY RATIONS (according to Mitchell, 1947)

Growing pigs				*Pregnant sows*			
Body weight lb.	*Calcium required*	*Phosphorus required*	*Ca : P ratio*	*Week of gestation*	*Calcium required*	*Phosphorus required*	*Ca : P ratio*
75	0·63	0·35	1·8	10	0·10	0·19	0·6
100	0·59	0·33	1·8	11	0·14	0·20	0·7
150	0·52	0·31	1·7	12	0·18	0·21	0·8
250	0·38	0·26	1·5	13	0·23	0·23	1·0
350	0·24	0·21	1·1	14	0·28	0·24	1·2
450	0·09	0·13	0·7	15	0·34	0·27	1·3
500	0·05	0·10	0·5	16	0·43	0·29	1·5

The deficiency of calcium manifests itself in weakness of the skeleton, due to impaired or distorted bone growth, stiffness, lameness, paralysis and fractures of bones (*Figures 2.18* and *2.19*). Rickets is usually due to imbalance between Ca, P and vitamin D in the ration. In young

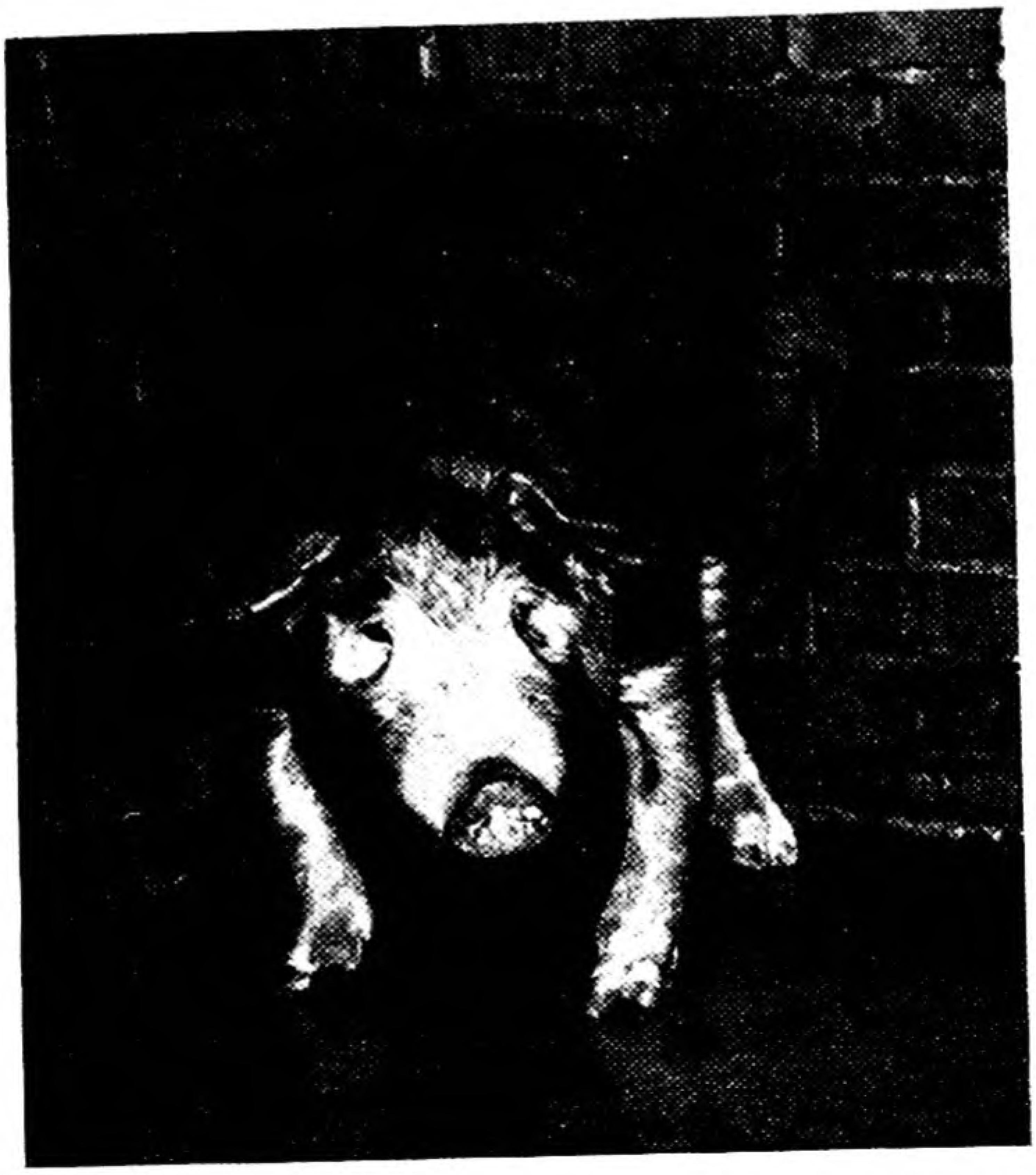


Figure 2.18. Pig with leg condition resulting from calcium and phosphorus deficiency. This pig was fed a ration containing 0·3% calcium and 0·2% phosphorus. (By courtesy of Professor D. V. Catron, Iowa Agr. Exp. Station.)

pigs true rickets, while in older ones osteoporosis is usually encountered. The plasma calcium falls below 5 mg. per cent. Pregnant sows on a calcium deficient diet become lame, have difficulties in farrowing and in raising their litters.

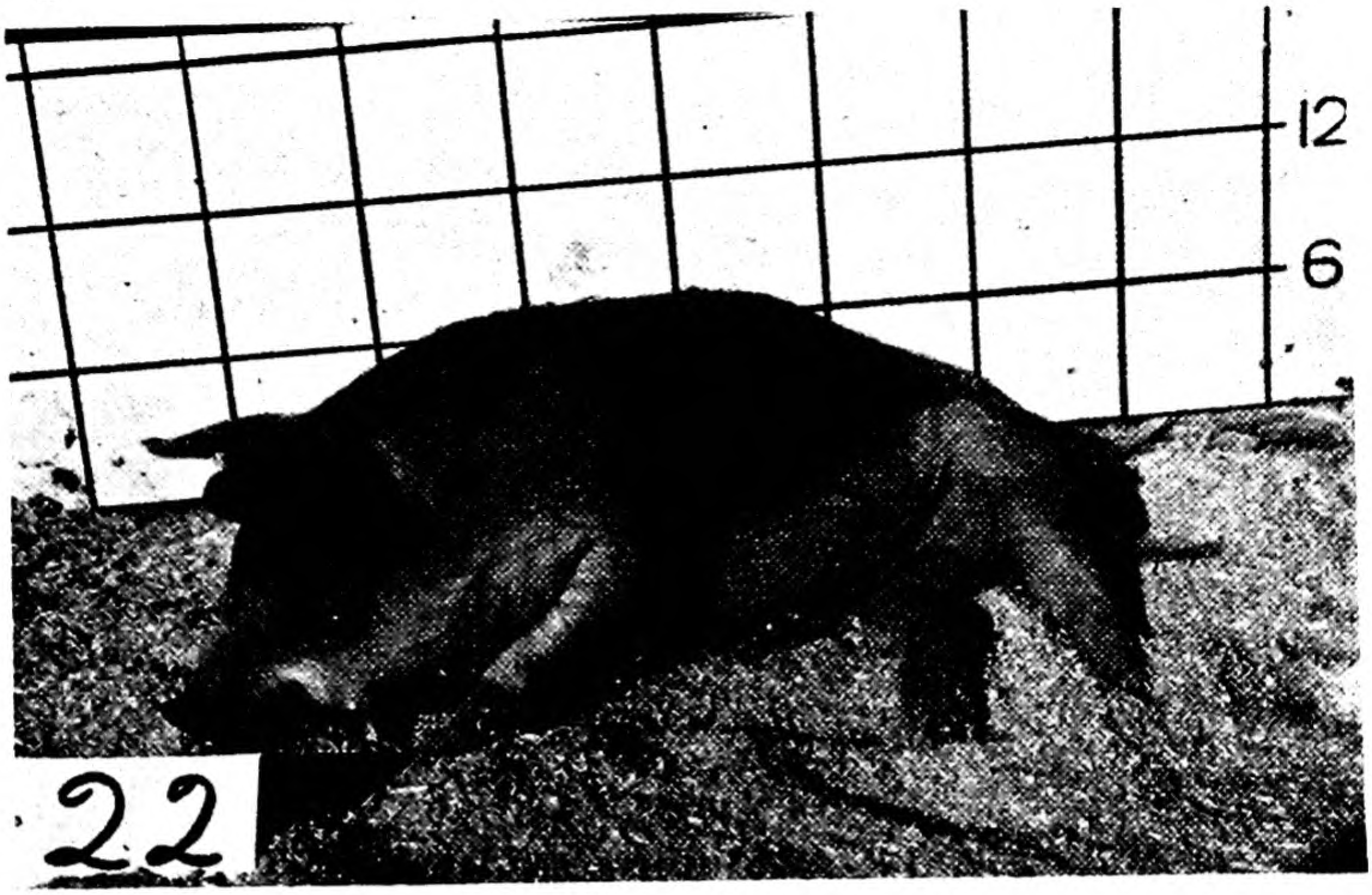


Figure 2.19. A pig with more advanced calcium and phosphorus deficiency. The pig's hind quarters were paralysed and it was unable to stand. (By courtesy of Professor D. V. Catron, Iowa Agr. Exp. Station.)

Deficiency of phosphorus is responsible for the bone disease osteomalacia, manifesting itself in a failure of calcification, and a malformation of bones.

The amount of phosphorus present in the cereals, and their by-products, which usually form the bulk of the rations for pigs, is quite adequate to meet the requirements. The fact that a large proportion of the element is present as phytin-phosphorus, which may not be available to the animal, does not affect this conclusion, as usually pig diets contain sufficient of the phytin splitting enzyme phytase. Under specific circumstances, however, the phytin content of the diet may require consideration, particularly if large quantities of maize or oats are fed, as these cereals do not contain phytase.

Adequate amounts of vitamin D are necessary for proper utilization of Ca and P, but it is important to realize that the presence of vitamin D will not compensate for the lack of these two vital elements.

The requirements for potassium are about 0·2% of the diet, for sodium 0·08% and for chlorine 0·12%. Common salt supplies sodium and chlorine in about right proportion for growing pigs (1:1·54). The salt requirements of growing pigs are well covered by the provision of 9 g. of salt per day for every 100 kg. live weight. On the same basis, the requirement of pregnant sows will be covered by 10–12 g., while that of nursing sows by 12–15 g. Sodium chloride, besides increasing the palatability of the food, has an important function in blood plasma and in the physiology of body cells. A low intake of salt causes retardation of growth, impaired efficiency of food utilization and a fall in the chloride level in blood plasma. About one-third of the total chloride content of the body is present in the skin and the tissue under it.

Although the pig's body contains a fair amount of magnesium, the indispensability of this element in rations for pigs has not been established as yet. It is unlikely that under normal feeding conditions a deficiency of magnesium should occur. It has been stated that the magnesium requirements are about 30 per cent of those for salt.

The quantitative requirements of pigs for iodine, which is essential for normal functioning of the thyroid gland, are not established, but a deficiency is not likely to occur except in areas where it is endemic. It has been suggested that a daily intake of 80–100 μg. of iodine will cover satisfactorily the requirement of a pig. This estimate was calculated, using as a basis the existing relationship between iodine requirement and heat production. A stabilized salt containing 0·01 per cent of iodine will correct any deficiency. Hairlessness, and thickened, pulpy, oedematous skin usually accompany iodine deficiency.

Fluorine should not be present in pig rations in more than a minute quantity. MITCHELL (1942) recommended that the permissible level of fluorine, which may be considered definitely safe under all conditions for long-time feeding, should be 0·003 per cent fluorine in the total ration. MAYNARD (1951) suggested 0·01 per cent fluorine as safe for short feeding periods.

The requirement of growing pigs for manganese is stated to be 12–20 parts per million. A deficiency, unlikely to occur under practical conditions, will impair growth and efficiency of food utilization, may cause lameness and enlargement of hock joints. On a ration containing less than 0·5 p.p.m. of manganese, reproduction was unsuccessful. It is interesting that a manganese supplement of 500 p.p.m. had a detrimental effect on growth rate and efficiency of food utilization.

Sulphur is an essential element and usually amply provided in normal rations. In inorganic form, such as flowers of sulphur, it is not assimilated by the pig, but rather through the amino acids, cystine and methionine.

Iron is an essential constituent of blood. It is concerned with the transport of oxygen and metabolism of food material within the cell. Deficiency of iron, however, is unlikely to occur under normal conditions of pig husbandry, except in a very young suckling pig. This deficiency is due to lack of iron in the sow's milk. During the time when a pig's diet is limited to sow's milk, anaemia will develop, unless the young pig has access to a source of iron. Venn, McCance and Widdowson (1947) found in their experiments that a piglet contains about 50 mg. of iron at birth, and that a piglet must retain about 7 mg. of iron per day to grow at a normal rate without becoming anaemic. The milk of the sow cannot be expected to supply more than 1 mg. per day. Sow's milk cannot be enriched in iron by feeding the mineral to the sows, as hardly any of it passes to the milk. It has been claimed that, by feeding high doses of iron to pregnant sows, 15 g. of ferrous sulphate per day, the foetuses were endowed with iron, and at birth the young had higher haemoglobin levels, which gave them a better chance of avoiding the development of anaemia during the suckling period. Incidentally, the average haemoglobin value for a pig is 12 mg./100 ml. of blood, the range being 8–16 mg./100 ml. The average normal hematocrit, a measure often used in anaemia studies in pigs, is 58 vol. per cent of RBC.

Usually, the simplest way to ensure an adequate intake of iron is to rear the pigs out-of-doors, where they get iron directly from the soil. Cases of the soil being deficient in iron are very rare indeed. When pigs are reared indoors a source of iron must be provided, and 15 mg. of iron per pig per day, during the second week of life, has given full protection against anaemia. There are various ways of administering iron to the suckling pigs, and various forms of readily available iron can be used.

A recent report claimed that anaemia can be produced in pigs through the mechanism of antigen-antibody reaction between the erythrocytes of the new born pig and the antibodies of the sensitized sow (a sow injected with the erythrocytes of the boar to which it was bred). The disease appeared in apparently healthy new born pigs after they obtained the specific erythrocyte destroying antibodies from the sow's colostrum (Bruner *et al*, 1949).

Copper is apparently essential for haemoglobin production and regeneration. The evidence of actual copper deficiency, however, has only recently been produced in pigs. Teague and Carpenter (1951) have produced copper deficiency in baby pigs, receiving a diet consisting of supplemented cow's milk. In addition to the blood deficiency, the pigs showed lack of rigidity in the leg joints, the fore legs showing various types and degrees of crookedness, resembling rickets (*Figure 2.19*). They did not respond to vitamin D treatment, but did respond to copper. While diets supplying 0·025 and 0·035 mg. copper per lb. of body weight produced deficiency symptoms, diets with 0·05 and 0·07 mg. did not.

Copper, like iron, is not present in sow's milk except in very minute quantities, and should be provided to the young pig in the same way as iron. It has been recommended that copper should be given at the rate of about 5 per cent of the iron given to prevent anaemia. Usually, the commercial iron preparations contain sufficient copper as an impurity, but a small quantity of copper should be added, should that not be the case.

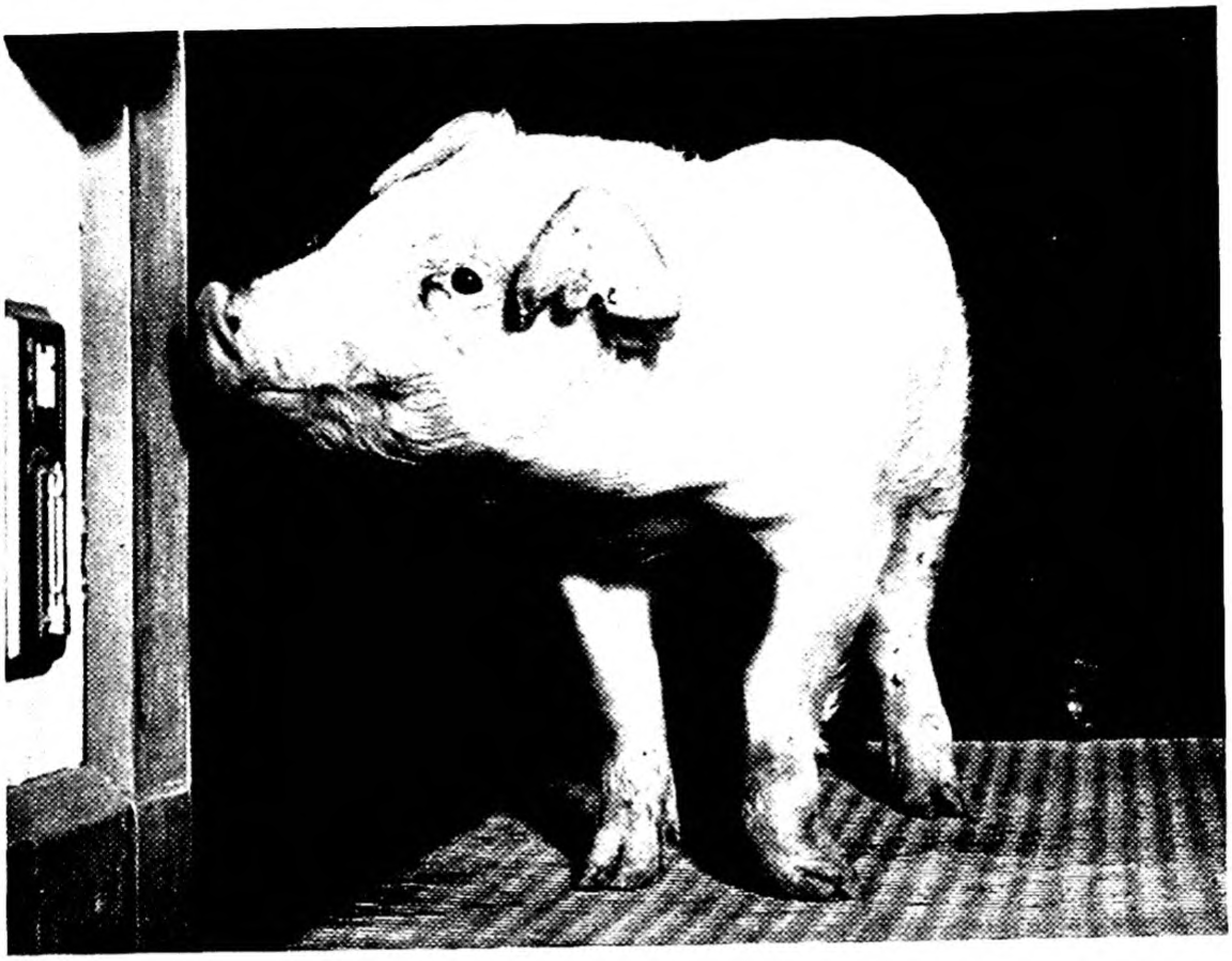


Figure 2.20. A pig showing signs of copper deficiency. (By courtesy of Dr. L. E. Carpenter, University of Minnesota.)

A craving for copper was observed in pigs receiving a normal diet, known to contain 5 p.p.m. of copper (BRAUDE, 1945 and 1948a). Pigs given a self choice of two diets, consumed considerably more of the one supplemented with copper. Recently, the preference for diets containing relatively high copper content was confirmed on suckling pigs having a choice of two creep meals (MITCHELL, 1953). This craving for copper may indicate that this element has some additional, as yet unidentified, function in the body, although its action as a catalyst in complicated enzyme reactions has been postulated. It is of interest that apparently the blood serum of pigs contains considerably more copper than that of cattle or sheep.

There is hardly any definite information available on requirements of pigs for other minerals. This is largely due to the fact that the amounts needed are so small that ordinary rations are never deficient in them, and preparation of experimental diets sufficiently poor in them is impossible in practice. The part played by so-called trace elements in physiological processes is mostly obscure, but judging by the extremely small quantities required, they are most probably of a catalytic nature. Evidence is accumulating to indicate that they are indispensable constituents of some intracellular enzyme systems.

The recent discovery that cobalt forms a part of the molecule of vitamin B_{12} revived interest in trace elements. Results of a number of tests indicated that weight gains of pigs can be increased significantly by supplementing a maize-soya bean diet with a trace mineral mixture consisting of cobalt, manganese, zinc, copper and iron. More evidence is required to substantiate these results, and also to prove that these findings are applicable to diets used in this country.

OTHER NUTRITIONAL FACTORS

UNIDENTIFIED FACTORS

From time to time reports have been published concerning positive effects on growth and/or food utilization, and/or reproduction, due apparently to nutritional factors, the identity of which has not yet been established. Claims have been made that skim milk, whey (either liquid or dried), lucerne meal, fish solubles, yeast, liver, molasses, and grass juice, contain an unidentified factor affecting the performance of pigs, particularly young ones. The existing evidence, however, is very limited, and one should reserve judgment on these factors until further research will either substantiate or refute these claims.

ANTIBIOTICS

JUKES *et al* (1950) reported results of an experiment indicating that the addition of a small amount of the antibiotic aureomycin to the rations of fattening pigs promoted their growth and improved the efficiency with which they utilized food. Since then, experiments carried out in many countries have confirmed this finding. BRAUDE, WALLACE and CUNHA (1953) have reviewed the field of antibiotics as growth promoters concerning pigs, and a review by BRAUDE, KON and PORTER (1953), which covers all the species, discusses the available information on the present-day knowledge of the mode of action of these antibiotics. The latter is as yet unknown, and a number of hypotheses are being investigated. It is quite probable that antibiotics can act in several ways, according to the conditions under which they are used. From the evidence available, it appears most likely that the antibiotics exert their effect by influencing the microbial population of the digestive tract. An attractive hypothesis based on some evidence that the intestinal walls in chicks and pigs receiving antibiotics are markedly thinner than in the control animal, has recently been put forward. Through the thinner wall more nutrients may be able to pass from the intestines, and thus the utilization of the ingested food may be enhanced.

At this stage of development perhaps the best one can do is to summarize briefly the established facts concerning the feeding of antibiotics to pigs. Aureomycin, bacitracin, penicillin and terramycin have, both under experimental and practical conditions, promoted the growth of pigs and improved their food utilization. An average increase in the rate of gain of about 10–15 per cent, and about 3–5 per cent improvement in the efficiency of food utilization were obtained. In some experiments, less than 10 per cent out of a total of several hundreds, no effect was obtained. The lack of response has not been satisfactorily explained. Streptomycin was found effective only under some experimental conditions; the effect of chloromycetin was rather doubtful ; neomycin, polymyxin, nisin and rimocidin (the anti-fungi antibiotic) were found not effective in several trials.

There is some evidence that the quality of the diet influences the results. On diets containing only vegetable protein a better response was obtained than on diets containing mixed vegetable and animal protein. On diets containing skim milk a smaller response was obtained than on diets without it.

It has been suggested that the degree of response is controlled by the extent of bacterial " contamination ". In some cases in which clinical signs of some disease of bacterial origin were present, the response to the antibiotics was more marked. Conversely, it has been suggested that under excellent hygienic conditions of pig husbandry the effect of antibiotics, if any, is rather small. There is also some evidence, confirming the finding with chicks (Coates *et al*, 1951) that in new piggeries, where pigs have not been kept before, there is no response to antibiotics. These arguments lead to the " disease level " hypothesis, suggesting that the effect of the antibiotics is due to the overcoming of either a clinical or a sub-clinical infection.

After scrutinizing all available evidence, one is led to the conclusion that the addition of antibiotics to the diet of pigs can serve a useful purpose, provided the economics of such a procedure are sound. Unfortunately, the long term effects, particularly on breeding stock, are as yet unknown, and therefore some caution is needed in the administration of these potent drugs to animals intended for breeding.

The amount of antibiotics recommended for fattening pigs is 5–10 g., for creep mixtures 15–25 g., and for milk substitutes 30–50 g. per ton of air dry mixtures. Recently the authorities in Great Britain have set by law the minimum quantity of antibiotics which must be included in compound mixtures. These are: 4 g. for fattening pigs, 5 g. for weaners and 10 g. for suckling pigs. Although the American evidence tends to give preference to aureomycin and terramycin, under British conditions, aureomycin and penicillin have given very similar results. There appears to be no advantage in feeding a mixture of two or more antibiotics as compared with a single one.

Evidence is accumulating, pointing to the fact that antibiotics exert their most marked effect on a young, fast growing animal, and that as the animal gets older the effect diminishes. Withdrawal of the antibiotic from the diet, after it has been fed to the animal for some time, appears to cause a setback, and although the response to antibiotics in the latter stages of fattening is smaller than in the earlier ones, it is probably a sound practice to continue the supplement throughout the fattening period.

The antibiotics exert a very beneficial effect when included in the rations of runt pigs. The level of feeding antibiotics to runts should be higher than that recommended for fattening pigs, 10–25 g. per ton giving a good response. In some cases the effect is dramatic ; pigs which appear unlikely to survive become normal in a short period of time, thus avoiding many losses. However, even in the case of runt pigs the general picture is rather marred by the fact that for unknown reasons, a small percentage of animals fail to respond to the treatment.

As far as milk substitutes are concerned, the advent of antibiotics made their application possible on a practical scale. All effective milk substitutes contain an antibiotic, and attempts to rear pigs artificially on a practical scale without it have hitherto failed.

SURFACE ACTIVE AGENTS

Recently claims have been made that some types of surface active compounds exert a growth promoting effect, similar to that of the antibiotics. Investigations followed a report by ELY (1951) showing that surface active agents stimulated the growth of chicks. LUECKE, HOEFER and THORP (1952) were the first to report a similar effect on pigs ; they used Ethomid C-15. Since then several contradictory reports have been published concerning the latter and other surface active compounds. Alkyl benzene sulfonate had a good response in one trial, when added to the ration at the level of 0·2 per cent. It has been said that there are about two thousand different surface active agents which may be potential growth promoters. About one hundred of these have already been tested, mainly with disappointing results. It has been suggested that these compounds may act in a similar way to the antibiotics, namely through a specific effect on the microbial flora of the digestive tract, or through increasing the absorption of nutrients from the intestines. It has been established that there is no synergistic effect between surface active agents and antibiotics.

ARSENICALS

During the last few years it has been noted that 3-nitro-4 hydroxy phenyl arsonic acid stimulated the growth of pigs (CARPENTER, 1951). The drug was fed at 0·05 per cent of the diet. However, these results were not confirmed by subsequent workers, and it is of interest that

BECKER *et al* (1952) found that, when the drug was fed in conjunction with antibiotics, it did not exert a significant complimentary effect. Although it has been proved that arsenical compounds are quite safe for both the animal and the consumer of animal products at the low levels fed in laboratory experiments, at higher levels these substances are so highly toxic that their use in animal feeding practice would be fraught with great danger and ought not to be encouraged. It is interesting to note that livers from pigs fed a diet containing 0·005 per cent of the arsenical contained 1·69 μg. of arsenic as As_2O_3 per g. fresh tissue, compared with 0·19 μg. in livers from control animals.

ENDOCRINE STIMULANTS

During the last few years attempts have been made to stimulate the growth of pigs and improve their food utilization by various substances affecting the endrocrine system of the pig. Within the scope of this chapter it is only possible to give a few references to act as an introduction to a study of this subject.

Thyroid-active substances and anti-thyroid drugs.—It has been suggested that a mild hyperthyroid condition may be conducive to rapid growth. Iodinated protein and synthetic thyroxine have been used in order to induce hyperthyroidism. REINEKE and McMILLEN (1946), BEESON *et al* (1947 and 1949b), WALLACH *et al* (1947), REINEKE, McMILLEN and BRATZLER (1948), PERRY, BEESON and ANDREWS (1950), by including small amounts of iodinated protein in the diet, have increased the growth rate of pigs and improved efficiency of food utilization. BRAUDE (1947a), MUHRER *et al* (1947) and VAN DER NOOT, REECE and SKELLY (1948), however, obtained negative results. As a possible explanation of the recorded discrepancies, it has been suggested that positive results can only be obtained when the level of the iodinated protein decreases in proportion to live weight as the pigs grow in size.

The levels of iodinated protein effective in some of the tests were: 0·005, 0·0075, 0·0088, 0·0132 and 0·0176 per cent of the diet. In one test, however, 0·1 per cent produced adverse effects, and so did 1·5 g. per day given at a constant level.

There exists a controversy concerning the age at which iodinated protein fed to pigs may be most effective. BLAXTER *et al* (1949) stipulate that iodinated protein will only be effective if given during the early growth stages, while PERRY, BEESON and ANDREWS (1951) claim no response until the pigs reached about 130 lb. live weight.

There is some evidence that in hyperthyroidism there is a need for additional nutrients. Addition of vitamin B_{12} was tried by several workers (*cf.* BARBER, BRAUDE and MITCHELL, 1953b) without conclusive results. SWICK, GRUMMER and BAUMAN (1952) reported that the stores of vitamin A in the liver were not affected by feeding iodinated protein.

It is interesting to note that feeding iodinated protein, on levels effective indoors, produced no effect on pigs on pasture.

Following the evidence that milk production of a cow can be increased substantially by feeding iodinated protein, two rather inconclusive attempts were made to test the effect of iodinated protein on lactating sows, Reineke and McMillen (1946), Braude (1947a), without producing definite confirmation. Any stimulation of the milk yield of the sow, especially during the critical stage, when the peak of lactation has been reached and the piglets have not yet taken to solid food, would be of great practical advantage.

A lowering of the thyroid function, associated with a decreased metabolic rate, is considered conducive to the fattening process, and goitrogenic substances, like thiourea, thiouracil and its derivatives, were tested with the object of studying their effect on the economy of fattening. These drugs produced extreme hypertrophy and hyperplasia of the thyroid gland in the pig. Following the over-optimistic report of MUHRER and HOGAN (1945), who claimed an increase in the rate of growth and efficiency of food utilization after the feeding of thiouracil, many workers used the different thio-drugs producing rather discordant results. The investigators are, however, agreed on one aspect, namely that if the drugs are given at too early an age, depression of growth results, often accompanied by signs of cretinism and myxoedema. If the drugs are given during the last 4–6 weeks of the fattening period (after the pigs have reached 150 lb. live weight), a substantial improvement in economy of gain, with little decrease in the rate of gain was recorded. There is controversy concerning the possibility of practical application of thiouracil in the latter stages of fattening. This controversy is well mirrored in the conclusions arrived at by the two British centres which investigated the problem. While BRAUDE and COTCHIN (1949) concluded that, though food utilization was slightly improved, the adverse effects of drugs on appetite and growth would make their use in pig feeding uneconomical, ROBINSON and COEY (1951) think that in view of the saving in meal observed, commercial exploitation should be considered. The levels at which the goitrogenic substances gave positive results were: for thiouracil 0·1, 0·2 and 0·25 per cent of the diet, for methyl thiouracil 0·05 and 0·1 per cent of the diet.

An attempt to combine the apparent beneficial effect of iodinated protein on younger pigs and thiouracil on older pigs, by feeding iodinated casein up to the weight of 150 lb. and follow it by thiouracil, gave inconclusive results (Van der Noot *et al*, 1948; Beeson *et al*, 1949b).

Sex hormones (*a*) *oestrogens.*—During the last few years attempts have been made to promote the growth of pigs by feeding synthetic oestrogens.

The possibility of effecting "hormonal castration" by feeding stilboestrol to boar pigs has been discounted, following the results of **BRAUDE** (1947b), **WALLACE** (1949) and **PEARSON** *et al* (1951).

DINUSSON, KLOSTERMAN and **BUCHANAN** (1951) and **WOEHLING** *et al* (1951), who implanted a 12 mg. stilboestrol pellet when the pigs were 12 weeks old, and followed with another pellet 12 weeks later, and Pearson *et al* (1951), who implanted a 25 mg. tablet into a pig weighing 35 lb., and followed it by a second implantation (25 mg.) after one month, and a third one (50 mg.) after two months, found no material effect on the rate of gain or efficiency of food utilization. On the other hand, **LETARD, SZUMOWSKI** and **THERET** (1952) reported acceleration in growth, following a single large injection of dienoestrol diacetate. They found that the effect was more marked on female pigs than on castrated males, but **COLE** *et al* (1952) found no effect from a single injection of either 50, 100 or 200 g. of dienoestrol in aqueous suspension. Pearson *et al* (1951), who implanted stilboestrol into females, found no adverse effects, while Braude (1947b) who gave stilboestrol orally, reported that treated gilts exhibited continuous oestrus and grew at a subnormal rate. **SLEETH** *et al* (1952), who injected 1 mg. of oestradiol/kg. body weight, found no effect on growth, but when given to gilts, swelling of the vulva and enlargement of the mammary glands occurred.

(*b*) *Androgens.*—It is well known that androgens exert a protein anabolic effect. Woehling *et al* (1951) and Dinusson *et al* (1951) implanted a 15 mg. pellet of testosterone, followed by another pellet after an interval of 12 weeks, and found no effect whatsoever. Similarly, Sleeth *et al* (1952) obtained no response following an injection of 1 mg./kg. body weight of testosterone propionate.

(*c*) *Combined treatment.*—**BRAUDE** (1948, 1950) and Barber *et al* (1953b) reported that, when castrated male pigs were given orally 500 mg. iodinated casein and 30 mg. stilboestrol daily, or 0·3 mg. l-thyroxine and 6 mg. stilboestrol/lb. of diet, the pigs grew faster and utilized their food more efficiently than control litter mates. Barber *et al* (1953b) also recorded a considerable enhancement of the effect by including aureomycin in the diet.

General remarks.—A critical survey of the attempts to influence growth by the use of endocrine stimulants leads one to the conclusion that the results as yet obtained do not justify application in practical pig keeping. However, what emerges quite clearly from the survey is the usefulness as well as the limitations of these substances, and certainly investigations of this kind mark an advance in our knowledge of the physiological processes upon which pig production is based. The evidence on the effectiveness of the endocrine stimulants available at the present time is confusing and often contradictory. Many difficulties arise from our inability to control the active substances within the body.

It appears that a balance between endogenous and exogenous stimulants must be attained in order to obtain results which would promise to be useful in practical pig husbandry. The rate of hormone secretion in an animal appears to be an individual characteristic, probably inherited, but there can be no doubt that it is also influenced by environmental factors, such as temperature, light, nutritional status, etc. The study of these interrelationships has hardly yet begun.

BAIRD, NALBANDOV and NORTON (1952) examined the growth hormone of anterior pituitaries from 56 pigs belonging to two genetically different lines selected for rapid and slow growth. They found pituitary and thyroid weights to be related to the weight of the pigs. At all ages anterior pituitaries from the rapidly growing line contained significantly higher amounts of growth hormone per unit tissue than did the same amount of tissue from the slow growing line. There were no significant differences in sexes. In relation to anterior pituitary size and body weight, the amounts of growth hormone increased up to a certain age and then decreased until mature size was reached. The authors suggested that growth is regulated by the amount of circulating growth hormone. As the animal grows older and gets bigger, the amount of hormone does not increase at the same rate, and eventually growth stasis sets in, due to insufficiency of the hormone in relation to body weight.

There is one further point to emphasize concerning a possible use of endocrine stimulants for promoting growth. Before the usefulness of drug treatment for increasing production of pig meat is seriously considered, one would have to be satisfied that the meat from treated animals is safe for human consumption. Braude (1950) provided evidence that meat from pigs fed stilboestrol had no oestrogenic activity. On the other hand, LETARD *et al* (1952) proved that when synthetic oestrogen dienoestrol diacetate was injected into a pig, the tissues, especially the fat, contained considerable amounts of active oestrogenic substances.

RADIOACTIVE ISOTOPES

During the last few years a new tool became available for studies of a fundamental nature in the field of biology and medicine—the radioactive isotopes. In their application to problems involving pigs, a start has been made, and a few references to published reports are given below. SMITH *et al* (1951) has studied the distribution of intravenously injected radioactive phosphorus, P^{32}, among pig tissues. COMAR, LOTZ and BOYD (1952) reported on deposition and removal of Ca^{45}, P^{32} and Sr^{90} from the skeleton of the weaner pig, and COMAR, VISEK, LOTZ and RUST (1952) studied the effect of fluorine on skeletal metabolism and bone growth in pigs as shown with radioactive calcium, Ca^{45}.

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CHAPTER 3

POULTRY

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THIS chapter is presented as a survey of recent advances in poultry nutrition and metabolism and not as a critical review of all the work carried out in this field; indeed, the latter task could not be accomplished in a single chapter.

Some sections have been reviewed within the past few years, such as the vitamins by HOGAN (1949) and the minerals by TYLER (1948–9); in others, such as vitamin B_{12} by SMITH (1950–1), poultry have been considered in conjunction with other animals, including man.

In the United States of America, the National Research Council appointed a sub-committee to sift and collate information on the nutritive requirements of poultry. This sub-committee issued its first report in 1944, and revised reports appeared in 1946 and 1950. The allowances for vitamins in these reports consist of a requirement value agreed upon by the sub-committee plus an arbitrary ‘ margin of safety ’, which is 66 per cent for vitamin A, 45 per cent for cholecalciferol and 20 per cent for the water-soluble vitamins, to cover variations found within meals and losses by destruction. Tables 3.5, 3.7, 3.8, 3.10 and 3.12 in the chapter are taken from the 1950 report.

THE DIGESTIVE TRACT

This has been fully described by HALNAN (1949) and by BRADLEY (1950); it is sufficient, therefore, merely to mention it briefly.

The digestive tract of the bird consists of a hollow tube running from the mouth to the cloaca, modified along its length into characteristic organs. Starting from the mouth, these organs are named the pharynx, oesophagus, proventriculus, gizzard, duodenum, small intestine, large intestine and cloaca.

The mouth is devoid of lips or teeth. These are replaced by a pointed, horny beak, the lower section of which is joined to the skull *via* the quadrate bone, thus permitting a very wide distension of the mouth opening. There is no clear line of demarcation between mouth and pharynx and the pharyngeal region is regarded as extending from the posterior end of the hard palate to the anterior end of the oesophagus. This latter is a distensible tube, enlarged in the interclavicular region to form a pear-shaped sac, the crop. The proventriculus, sometimes referred to as the glandular or true stomach, is richly supplied with gastric glands. It communicates with the gizzard or muscular stomach, a compact, oval structure composed of two thick lateral muscles in apposition to each other and two thin intermediate muscles. It is lined with a corrugated layer of keratin-like material.

The duodenum forms a loop enclosing the pancreas and the three pancreatic and two bile ducts open into the alimentary canal at the junction of the duodenum and the small intestine. At the posterior end of the small intestine, where it is joined to the large intestine, two blind sacs, the caeca, are found. The large intestine communicates with the exterior through the cloaca, an orifice which serves the treble purpose of excreting faeces, urine and eggs or seminal fluid.

THE PROCESS OF DIGESTION

When a bird has been deprived of food to empty the crop and gizzard, the first few mouthfuls of food pass directly to the proventriculus and thence to the gizzard. Subsequently the food is stored in the crop. After a meal is completed the food in the crop is gradually transferred to the gizzard *via* the proventriculus. Meanwhile the gizzard is undergoing rhythmic contractions, grinding the food with moisture into a smooth paste which passes to the duodenum. Should food be present in the crop when the bird begins to feed, the gizzard is kept supplied by the new food and the surplus is added to the food already in the crop. It is thus most important that, when markers are used to measure food consumption, care should be taken to ensure that the crop is completely empty before feeding the marked diet, otherwise erroneous results may be obtained.

Once food reaches the duodenum it is propelled posteriorly by peristaltic contractions of the gut until it reaches the junction of the small and large intestines. At this point some of the liquid portion of the excreta is by-passed into the caeca. The nature of the caecal contents varies with the condition of the normal excreta. If this latter is fairly dry the caecal contents form a chocolate coloured, semi-fluid material, while if it is rather liquid the caecal contents resemble the contents of the large intestine.

Considerable absorption of the liquid of the urine occurs in the cloaca and the unabsorbed urinary residues appear as a white cap on the discharged faeces.

Saliva, secreted by glands in the mouth, is slightly alkaline and contains the enzyme ptyalin, which hydrolyses starch to sugar. This action continues in the crop, and most probably a limited fermentation of the food also takes place at this stage. In the proventriculus the food is mixed with the gastric secretions, containing free hydrochloric acid and the protein splitting enzyme pepsin. This hydrolysis of protein continues in the gizzard and duodenum, at the posterior end of which the alkaline secretions of the pancreas and the liver (the bile) are added to the food. The bile is an alkaline fluid containing lipase, an enzyme which hydrolyses fats, while the pancreatic fluid contains three pro-enzymes. These are acted upon by erepsin, an enzyme secreted by the walls of the small intestine, and released as the starch-splitting enzyme amylopsin, trypsin—which hydrolyses protein, and steapsin—which acts upon fat.

The food is thereby broken down into sugars, amino-acids or groups of these known as peptides, and free fatty acids. The free fatty acids and a certain amount of emulsified fats are absorbed by the cilli of the intestine communicating with the lymphatic system while the amino-acids, minerals and sugars are absorbed directly into the blood-stream.

That portion of the food which is not digested is excreted as faeces.

The whole process of digestion is rapid, an individual portion of food takes about two hours to pass through the small and large intestines, and a normal meal (*ca.* 60 g.) about twelve hours.

DIGESTIBILITY OF FOOD COMPONENTS

CARBOHYDRATES

Carbohydrates supply most of the energy in the diet, and chemically can be divided into five main groups: (*a*) Sugars. (*b*) Dextrins and starches. (*c*) Hemicelluloses, including galactans, pentosans, pectins and the polyuronides. (*d*) Celluloses. (*e*) Lignins.

The first step in any digestibility trial would, therefore, appear to be the use of methods capable of distinguishing between these components. Yet this is usually ignored, and results are expressed in terms of ‘ nitrogen-free extractives ’ and ‘ crude fibre ’, after carrying out the conventional feeding-stuffs analyses.

Norman (1935) showed that while crude fibre consisted almost entirely of cellulose and lignin it did not represent the whole of these two fractions. He found that only 40 per cent to 88 per cent of the cellulose and 4 per cent to 67 per cent of the lignin was recovered as crude fibre. In the materials he examined, the lowest recoveries in both cases were obtained with bran.

Lignin and cellulose are not digested by the fowl, although their inclusion in a diet gives valuable bulk and thereby assists digestion. The addition of 5–12 per cent cellulose to a diet free from indigestible material increased the growth rate, but increasing this to 20–25 per cent retarded growth.

It has also been shown that the digestible carbohydrates in coarse and fine bran are almost identical with the total of the starch plus sugar, as the figures in Table 3.1 illustrate.

TABLE 3.1

DIGESTIBLE CARBOHYDRATES AND TOTAL OF STARCH PLUS SUGAR IN COARSE AND FINE BRAN

	% N-free extractives digested	*Starch + sugar as % N-free extractives*
Coarse Bran	42·2	43·9
Fine Bran	57·0	58·4

From these results it would appear that the hemicellulose component is not digested by the fowl, and that the determination of the value for starch plus sugar, with the residue classed as non-digestible carbohydrate, would be much more informative than the conventional method of determining crude fibre and calling the residue nitrogen-free extractives.

The growth-promoting properties of some carbohydrates have been investigated, and the nutritional efficiency decreased in the following order: dextrin, glucose, sucrose and lactose. Lactose was unsuitable as the sole carbohydrate in diets for laying hens.

In the ‘ High energy diets ’ recommended for broiler production in the U.S.A., it is noteworthy that the amount of indigestible material has been drastically reduced compared to the diets normally fed to poultry, as the two formulae given in Table 3.2 illustrate.

TABLE 3.2

HIGH ENERGY DIETS

	Connecticut lb.	*Washington lb.*		*Connecticut lb.*	*Washington lb.*
Maize meal	71·84	69·51	Nicotinic acid	900 mg	—
Alfalfa meal	1·00	1·00	Limestone flour	1·45	2·20
Herring meal	5·95	6·80	Common salt	0·50	0·50
Meat meal	6·84	—	Ca_2HPO_4	0·24	0·91
Soyabean meal	6·82	17·00	Iodized $MnSO_4$	0·025	0·025
Liver meal	3·00	1·00	Vitamin A & D Supplement	0·06	0·06
Fermentation products (500 µg/g riboflavin)	2·00	1·00	Analysis:		
Choline premix	0·28	—	Crude protein	21·0	21·0
			Ca	1·4	1·4
			P	0·7	0·7

FATS

The ingestion of fat provides the fowl with its other main source of energy, yet again this field has been virtually neglected. It has been found that certain of the poly-unsaturated fatty acids cannot be synthesized by the bird and must be supplied in the diet. On fat-free diets moribund chicks are encountered and these are frequently oedematous, the subcutaneous layers having the appearance of a clear jelly.

Fat can be synthesized from carbohydrate, and although thiamine is required for the metabolism of carbohydrate to energy, pigeons force-fed a diet of thiamine-free carbohydrate showed no impairment of fat synthesis, indicating that thiamine is not necessary for this process. Chicks digest and tolerate high levels of fat. Linseed oil (12 per cent) was digested more efficiently than mutton fat, showing that although the body temperature of the chick is relatively high, this does not enable it to digest fats of high melting points as efficiently as oils. When high levels of cottonseed oil, lard or hydrogenated vegetable oil were added to a diet low in riboflavin, the cottonseed oil, but not the lard or the hydrogenated vegetable oil, retarded the growth of the chicks. This effect was ascribed to the interference of the unsaturated fatty acids with the intestinal synthesis of riboflavin.

Mature fowls have been fed diets containing levels of fat as high as 30 per cent without ill effect. However, as is discussed under vitamin E, high levels of fat are not recommended in poultry diets, since the development of rancidity can destroy the vitamin E in the diet.

PROTEINS

The crude protein content is ascertained by determining the total nitrogen of the sample and multiplying this, expressed as a percentage, by 6·25; it is therefore assumed that all proteins contain 16 per cent nitrogen. Whilst this is not strictly true, as Table 3.3 illustrates, it is sufficiently accurate for feeding-stuffs analysis, particularly since it is now realized that the crude protein content is of minor importance compared to the amino-acid content.

TABLE 3.3

TABLE OF FACTORS FOR CONVERSION OF % NITROGEN TO % PROTEIN

Barley	5·82	Blood	5·80
Oats	6·31	Maize gluten meal	5·70
Buckwheat	6·25	Rye	5·62
Meat	5·80	Maize	6·39
Casein	6·25	Wheat and wheat products	5·70
Milk	6·38		

This factor, however, cannot be used to calculate the amount of nitrogenous material in poultry excreta since, as has already been mentioned, poultry excreta is a mixture of faeces and urine. Only about one-quarter of the nitrogen is faecal nitrogen, and of the urinary nitrogen, by far the largest moiety is present as uric acid.

The apparent digestibility of nitrogen is given by the formula

$$\frac{\text{N in food} - \text{N in faeces}}{\text{N in food}}$$

and the true digestibility by

$$\frac{\text{N in food} - \text{N in faeces} - \text{Endogenous faecal N}}{\text{N in food}}$$

It is apparent, therefore, that some means must be devised for separating the faecal and urinary nitrogen in poultry excreta before the digestibility of nitrogen can be determined. The methods suggested fall into three groups.

(1) Artificial anus

By exteriorizing the large intestine to an artificial anus the faeces and urine can be collected separately. However, even when the operation is successfully accomplished, and this is by no means easy, the results obtained cannot be regarded as relating to a normal bird.

(2) Physical separation

Methods using physical separation usually depend on scraping the white crust of urinary deposits off the voided excreta. This is quite obviously inaccurate as it omits that portion of the urine absorbed by the faeces.

(3) Chemical separation

(*a*) *Indirect.*—In the indirect method the faecal nitrogen is estimated by subtracting the urinary nitrogen from the total nitrogen. It is manifestly impracticable to determine all the nitrogenous compounds in urine separately, so a compromise is effected. This consists of estimating the uric acid and sometimes the ammonia and multiplying these by a factor. The multitude of factors put forward is illustrated by the following selection.

$$\begin{aligned}\text{Urinary N} &= 1{\cdot}125 \text{ uric acid N}\\ &\quad\text{or uric acid N} + \text{Ammonia N}\\ &\quad\text{or } 1{\cdot}146 \text{ (uric acid N} + \text{ammonia N)}\\ &\quad\text{or } 1{\cdot}25 \text{ (uric acid N} + \text{ammonia N)}\\ \text{Faecal N} &= 1{\cdot}023\ [\text{total N} - 1{\cdot}146 \text{ (uric acid N} + \text{ammonia N)}]\\ &\quad\text{or } 1{\cdot}068\ [\text{total N} - 1{\cdot}167 \text{ (uric acid N} + \text{ammonia N)}]\end{aligned}$$

Indirect methods suffer from a disadvantage which cannot be overcome; since urinary nitrogen forms about three-quarters of the total nitrogen, the value for the faecal nitrogen is very much affected by the errors in the determinations.

(*b*) *Direct.*—The direct method of estimating faecal nitrogen has to surmount one main difficulty, that of converting the insoluble uric acid into some soluble compound or compounds without at the same time affecting the solubility of the faecal nitrogen. The methods suggested have included the use of dilute acids and mild oxidizing agents followed by the precipitation of the faecal nitrogen by the addition of a protein precipitant.

Faeces contain about 90 per cent true protein, and urine about 3 per cent. Since the ratio of faeces to urine is about 3 to 1, the determination of the true protein nitrogen in the faeces gives a good estimate of the faecal nitrogen, and the apparent digestibility can be calculated.

Before the true digestibility can be assessed, the endogenous faecal nitrogen must be estimated. This is done by feeding a diet free from nitrogen and measuring the faecal nitrogen output. Various values have been put forward, and a few of these, representative of different methods of determining the faecal nitrogen, are given in Table 3.4.

TABLE 3.4

ENDOGENOUS NITROGEN BY DIFFERENT METHODS

Method	*mg./day*
Artificial anus	86
Chemical separation (a) Indirect	143
(b) Direct	110

Urine collected from a bird with an artificial anus had a nitrogen content of 21·8 per cent of the dry matter. It would appear that in a digestibility trial the faecal and urinary nitrogen should be determined, the former multiplied by 6·25 and the latter by 4·59, and the total of these taken as the crude protein in the conventional analysis, otherwise the nitrogen-free extractives, a difference value, will be affected.

FOOD EFFICIENCY

The food eaten by the bird can be divided into two categories. First, the ' Maintenance Requirement ', the amount of food necessary to keep the bird alive and prevent it losing weight; and second the ' Production Requirement ', the excess of food ingested over the maintenance requirement which is utilized to produce meat, bone, eggs or feathers, etc.

The maintenance requirement increases with increase in the weight of the bird and it has been demonstrated that the bird uses 65 per cent of the food ingested in the first month for maintenance, 75 per cent in the second month, 80 per cent in the third, 85 per cent in the fourth and 90 per cent in the fifth. These data emphasize the need for full-feeding birds intended for sale as meat. On the other hand, age at maturity is not markedly affected by the size of the bird, so that economies in food can be effected by allowing pullets to grow at a slightly sub-optimal rate.

TABLE 3.5

FOOD (LB.) REQUIRED TO OBTAIN CERTAIN AVERAGE WEIGHTS WITH TWO DIFFERENT BREEDS

Average live-weight lb.	*Leghorns*			*Rhode Island Reds*	
	Female	*Male*	*Capon*	*Female*	*Male*
0·5	1·4	1·3	1·3	1·2	1·1
1·0	3·2	3·0	3·1	2·9	2·5
1·5	5·4	4·9	5·2	4·7	4·1
2·0	8·0	7·2	7·6	6·9	5·7
2·5	11·2	9·9	10·4	9·3	7·5
3·0	15·6	13·3	13·8	12·1	9·5
3·5	22·0	17·9	18·5	15·5	11·7
4·0	—	24·8	24·5	19·5	14·1
4·5	—	39·8	35·2	23·4	17·0
5·0	—	—	—	27·5	20·3

Males are more efficient converters of food into meat than are females, as the data in Table 3.5 indicate. It may be noted that in this Table, a White Leghorn cockerel requires 13·3 lb. food to reach 3·0 lb. live-weight, yet numerous reports in the literature indicate this live-weight can be achieved for the consumption of about 9·0 lb. food, *i.e.* the efficiency of food conversion can be increased by suitable diets from 0·23 to 0·33 lb. live-weight increase per lb. food.

This Table also indicates that to reach a given live-weight, the heavy breeds are more efficient than the light breeds, Rhode Island Red cockerels required only 9·5 lb. food to reach 3 lb. live-weight compared to 13·3 lb. for White Leghorns, an increase in efficiency of 0·09 lb. live-weight per lb. food.

The efficiency of food conversion is affected by the genetic constitution of the bird. This factor has assumed increased importance in the U.S.A., due to the rapid expansion of the broiler industry. For this industry the high energy diets (*see* Carbohydrates) have been developed, and in it the use of the antibiotics has been widely adopted. The addition of these antibiotics not only increases the rate of live-weight gain of the bird, but also its efficiency of food conversion, as the data set out in Table 3.6 illustrate.

TABLE 3.6

LIVE-WEIGHT GAIN AND EFFICIENCY OF FOOD CONVERSION DUE TO ADDED ANTIBIOTICS

	Average gain 2–4 weeks	*lb. gain/lb. food*
Complete diet	128	0·436
Complete diet + Antibiotic	134	0·457

LAYING BIRDS

Whether a hen is laying or not, it must still be supplied with sufficient food to meet its maintenance requirement. Each egg laid requires a certain amount of food, estimated at about 40 g. per 2 oz. egg. It is self-evident that the greater the rate of production of eggs, the more efficient the hen will be in food conversion. It is known that heavy breeds require more food for maintenance than light breeds, and Table 3.7 sets out the food requirements for different weights of bird at different rates of production.

TABLE 3.7

FOOD REQUIRED BY HENS AT DIFFERENT LEVELS OF PRODUCTION

Average live-weight (lb.)	*Total food (lb.) required for maintenance and the production of the indicated number of eggs per year*			
	Eggs 0	*100*	*200*	*300*
3·0	47	61	75	89
3·5	52	67	81	95
4·0	57	71	85	99
4·5	61	75	89	104
5·0	65	80	94	108
5·5	70	84	98	112
6·0	74	88	102	116
6·5	78	92	106	120
7·0	81	96	110	124

The addition of antibiotics to a laying bird's diet does not improve the efficiency of food conversion, and in this respect the laying hen differs from the growing chick.

With breeding stock, efficiency of food conversion must be carried a stage further, and the efficiency with which a bird can transfer the accessory food factors to the egg becomes important. The more important vitamins, vitamin A, cholecalciferol and riboflavin, have been studied and in a normal breeder's diet, about 25 per cent of the food nutrient is transferred to the egg. An increase in the dietary content reduces the efficiency of transfer. When the breeder's diet contains 5·1 μg. riboflavin per g. food, maximal storage is obtained in the egg; but with vitamin A and cholecalciferol, ceiling values, if they exist, have not been reached.

PROTEIN REQUIREMENT AND METABOLISM

The ingestion of protein provides the bird with its only source of nitrogen, an essential constituent of flesh, bones, skin, feathers and all other living tissues. When protein is fed in excess of the metabolic demand it can be de-aminated and utilized for energy production or for fat synthesis, but since protein foods are generally more expensive than carbohydrates, the determination of the minimal requirement has an economic significance.

Proteins can be hydrolysed into amino-acids, some of which can be synthesized by the fowl (the non-essential amino-acids) and some of which cannot (the essential amino-acids). These latter comprise arginine, cystine or cysteine, glycine, histidine, iso-leucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophane, tyrosine and valine, and the relative proportions of one to the other vary with different proteins.

Although in general terms it is true that the requirement for protein is greater in early life, when growth is most rapid, and gradually declines as the bird matures, the demand for protein is in reality a demand for the amino-acids in the correct proportions, and should one or more of these amino-acids be present in sub-optimal amounts, the rate of growth is controlled by that amino-acid and not by the content of total protein.

The determination of the amino-acid requirements of chicks is straightforward. Groups of chicks are reared on diets adequately supplied with all nutrients except the amino-acid under examination. Graded amounts of this amino-acid are added to the diets of the various groups and the minimal requirement is given by the lowest level supporting maximal growth. The values given in Table 3.8 for the minimal requirements were obtained by this method.

TABLE 3.8

RECOMMENDED ALLOWANCES OF AMINO-ACIDS FOR CHICKENS
(0–4 WEEKS OF AGE)

Amino-acid	*% of diet*	*Amino-acid*	*% of diet*
Arginine	1·2	Leucine	1·4
Methionine	0·9	Phenylalanine	1·6
or		or	
*Methionine+	0·5	†Phenylalanine+	0·9
Cystine	0·4	Tyrosine	0·7
Lysine	0·9	Threonine	0·6
Tryptophane	0·25	Valine	0·8
Histidine	0·3	Iso-leucine	0·6
‡Glycine	1·0–1·5		

* Cystine will replace methionine so long as the diet contains not less than 0·5% methionine.
† Tyrosine can replace phenylalanine so long as the diet contains not less than 0·9% phenylalanine.
‡ The chick can synthesize glycine but not at a sufficient rate for maximal growth.

With laying hens the problem is much more difficult. All attempts to maintain egg production on diets where the protein was replaced by amino-acids or by protein hydrolysates have been unsuccessful and the birds stopped laying in about four days. Even feeding 5 per cent casein suitably supplemented resulted in the cessation of egg production. The procedure adopted has therefore been to use as protein supplement some protein known to be low in the amino-acid under test and add this to the diet in graded doses.

Of the thirteen essential amino-acids, eight are found in adequate amounts in almost all proteins, so that the requirements for only five can be estimated by this method. These are set out in Table 3.9.

TABLE 3.9

AMINO-ACID REQUIREMENT FOR LAYING HENS AS % OF DIET

Leucine	1·35	Methionine	0·28
Tryptophane	0·15	with	
Lysine	0·52	Cystine	0·25

FACTORS AFFECTING THE REQUIREMENTS FOR AMINO-ACIDS

The amino-acid requirement will vary with the level of protein fed, and the relative proportions of amino-acids are more important than the protein level throughout the range of dietary adequacy from subnormal to super-normal protein levels. There is evidence indicating that when the demand for some of the amino-acids, *e.g.* lysine, is expressed as a percentage of the protein fed, the value decreases as the protein level increases.

When the chick is very young, the demand for the sulphur amino-acids, required for the production of feathers, is high in all breeds, but light breeds, whose ratio of feather weight to live-weight is greater than heavy breeds, have a higher requirement than heavy breeds.

On the other hand, excess of amino-acids can cause a retardation in growth. Glycine may be taken as an example of this effect. The requirement for glycine at 20 per cent protein is 1·0 per cent if the glycine is fed as gelatin, edestin, casein, or glycylglycine and 1·5 per cent if fed as free glycine. The chick can tolerate 4 per cent glycine only if adequate nicotinic acid is fed, but at 8 per cent growth is retarded even in the presence of excess nicotinic acid. Similarly excess methionine has a depressant effect on growth, which can be overcome by additions of glycocyamine or serine to the diet.

Finally, additions of antibiotics to the diet decrease the requirement for amino-acids. It is unlikely that the actual demand by the bird is affected, so presumably the antibiotics act by suppressing bacterial growth or by facilitating the absorption of amino-acids by the intestinal tract.

EGG PROTEINS

Diet does not affect the amino-acid content of the egg proteins, although sub-optimal levels of amino-acids in the diet can affect the rate of production. During incubation the amount of arginine remained constant. Methionine decreased by about 24 per cent, and this was accompanied by a 22 per cent increase in cystine. It was therefore suggested that two molecules of methionine were converted into one of cystine by the developing embryo. It is well known that tryptophane acts as a precursor of nicotinic acid, and injections of tryptophane into eggs were followed by increases in the nicotinic acid content of the embryos.

Of the non-essential amino-acids, the content of glutamic acid remained constant, while those of proline and hydroxyproline increased by 48 per cent.

AVAILABILITY OF AMINO-ACIDS IN PROTEINS

The availability of lysine and methionine was low in commercial cotton seed meals. The use of special solvents or removal of the gland increased their availability, suggesting that either gossypol or cotton seed oil was exerting the adverse effect.

Soya-bean meal contains a tryptic inhibitor which is destroyed by heat. Mild autoclaving or steaming increased the availability of the cystine and methionine present in soya-bean meal, presumably by the destruction of the tryptic inhibitor, although autoclaving at 130° C. for 1 hr. again reduced it. When soya-bean meal was autoclaved with carbohydrate, between 24 and 79 per cent of the methionine was destroyed or otherwise converted into a form from which it could not be liberated by enzymic hydrolysis *in vitro*. Lysine was also destroyed by autoclaving with carbohydrate, but the commercial preparation of groundnut meals did not affect the availability.

METABOLISM OF AMINO-ACIDS

This field of study has been largely neglected. Studies with isotopic carbon have shown that the methyl group of methionine could be utilized by the chick in the synthesis of choline, and that glycine was a precursor of ribonucleic acid.

Folic acid additions *in vitro* enhanced methionine formation in livers from folic acid replete chicks, but not from folic acid deficient chicks.

Chicks could utilize pentahomoserine or citrulline, but not ornithine, for the synthesis of arginine. This indicated that the Krebs-Ormstrom urea cycle was incomplete in the fowl, although urea was present in the urine.

When cobalamin was deficient in the diet, the fowl could not utilize homocystine or homocysteine plus betaine to synthesize methionine, although it could do so when the diet was adequately supplied with cobalamin. This suggested that cobalamin is necessary for the transformation of homocystine to methionine.

It has been suggested that methionine acts as a decholesterolizing agent in old hens, and it is known that both methionine and choline function as methylating agents in poultry metabolism.

MINERAL REQUIREMENTS AND METABOLISM

Sufficient data has now been accumulated for the National Research Council to recommend nutrient allowances for the more important elements ; these recommendations are set out in Table 3.10.

TABLE 3.10

MINERAL REQUIREMENTS OF POULTRY

Mineral	*Chicks (0–8 wks.)*	*Growers (8–18 wks.)*	*Laying hens*	*Breeding hens*
*Calcium %	1·0	1·0	2·25	2·25
†Phosphorus %	0·6	0·6	0·75	0·75
‡Sodium Chloride %	0·5	0·5	0·5	0·5
Manganese p.p.m.	55	?	?	33
Iodine p.p.m.	1·1	0·66	0·66	1·1
Potassium p.p.m.	0·44	0·35	?	?
Magnesium p.p.m.	396	?	?	?
Iron p.p.m.	19·8	?	?	?
Copper p.p.m.	2·0	?	?	?

* The calcium need not all be fed as part of the mixed food since calcareous grits fed free choice are regarded as part of the diet.

† At least 0·4% of the phosphorus should be inorganic or non-phytin phosphorus.

‡ This value relates to added salt, it may require modification if meals high in salt, *e.g.* some fish meals, are used.

CALCIUM AND PHOSPHORUS

About 80 per cent of the phosphorus and 99 per cent of the calcium in the body is found in the skeleton. Nevertheless there is continual competition between the skeleton and the soft tissues, particularly those actively engaged in metabolic processes, for these two elements. If either is supplied in amounts insufficient to meet the demands of both skeleton and soft tissues, the soft tissues take priority over the bones.

The transfer of phosphorus from the soft tissues to bone is favoured by vitamin D and by optimal levels of fat in the diet, although excess fat may cause losses of calcium as calcium soaps.

Requirements

With an adequate supply of vitamin D and sufficient calcium and phosphorus, the Ca : P ratio may vary between 1 : 1 and 3 : 1 without adversely affecting bone formation. It is usually recommended that diets for chickens should contain 1·6 per cent calcium, 0·8 per cent phosphorus and 20 i.u. vitamin D per 100 grammes food.

Many experiments have been carried out using varying levels of calcium, phosphorus and vitamin D to determine the optimal amounts for calcification but as TYLER (1949) has pointed out, only a few of these were analysed statistically. Wide divergencies of opinion as to the best ratios have been expressed, and this may be partly due to failure to recognize that Ca : Total P. ratios are of little value, since about three-quarters of the phosphorus in cereals is present as phytin, a form in which it is not fully available to the chick for calcification. Field-cured alfalfa improves the utilization of phytin phosphorus by providing phytase, but this enzyme is destroyed by commercial dehydration. Vitamin D also increased the ability of the chick to utilize phytin-phosphorus, although there was no apparent difference when the phosphorus was supplied as inorganic phosphorus.

Tyler (1949) has summarized the existing situation in these words. ‘The level of vitamin D, the type of vitamin D and the type of phosphorus all influence the calcium and phosphorus requirements of chickens, and hence much of the earlier disagreement between workers was probably due to ignorance of these factors. A stage has now been reached where it is necessary to carry out large-scale co-operative experiments; these experiments would need to be of factorial design so that the influence of the several factors known to be involved would be defined by statistical analysis. Separate groups of workers, each group using its own basal ration and deciding what levels of calcium, phosphorus and vitamin D to feed, only continue to add to the confusion, particularly when statistical tests are ignored.’

Until the whole problem is solved, it is to be recommended that of the 0·8 per cent phosphorus in the diet, at least 0·4 per cent should be present as inorganic phosphorus. The levels recommended here are somewhat higher than those recommended by the National Research Council of the United States in 1950 for calcium and phosphorus but lower for vitamin D, and are the allowances suggested by Tyler (1949).

TABLE 3.11

CALCIUM AND PHOSPHORUS REQUIRED BY LAYING HENS

% *production*	*Calcium* % *of diet*	*Phosphorus* % *of diet*
100	4·60	0·38
50	2·74	0·32
0	0·39	0·25

The figures given in Table 3.11 show that it is not practicable to feed all the calcium required by laying hens in the diet; either the high producing hens will receive insufficient calcium or the poorer producers will have excess. The usual recommendation is that a level of about 1·0 per cent calcium should be included in the diet, and that oyster-shell or limestone grit should be available *ad libitum* in addition to the flint grit. It is unwise to omit the flint grit as then the bird, in its endeavours to keep sufficient grit in the gizzard, tends to consume more calcium grit than it needs, thereby imposing an additional strain on the digestive system.

Results from balance experiments

As already mentioned in the section on protein, balance experiments with poultry must perforce include the urine with the faeces, nevertheless they are capable of yielding much valuable information. Such experiments have shown that a bird stored calcium for about ten to fourteen days before coming into lay. Examination of the marrow cavities of the long bones showed that this calcium was stored as spicules, and that these could be seen so long as the bird continued to lay. In short term experiments the assumptions may be made that (*a*) changes in calcium and phosphorus during egg laying are related solely to the skeleton and (*b*) bone may be treated as a mixture of calcium orthophosphate with non-phosphatic or residual calcium. Balance data treated in this way showed that laying pullets receiving two grammes calcium per day as carbonate, gluconate or sulphate retained calcium from the food at a fairly steady rate of one gramme per day, with retention on laying days slightly exceeding that on non-laying days. On days of shell formation, when approximately two grammes of calcium were excreted as egg shell, the one gramme of calcium retained from the food that day would account for half that in the shell and the other one gramme must have been withdrawn from the skeleton. Since phosphorus excretion was relatively constant in these experiments, this gramme of calcium must have come from the residual or non-phosphatic calcium.

It has also been shown that shell secretion takes place at 113 mg. calcium per hour and with a diet containing 4 per cent calcium, calcium retention was 76 mg. per hour, showing that even with high dietary levels there must be a drain on skeletal calcium during shell formation. The bird can withdraw calcium from the skeleton at 66 mg. per hour, which is more than sufficient to cover the difference between the observed rates of retention and excretion.

Absorption and excretion

An analysis of food at different stages of digestion has shown that both calcium and phosphorus were leached from the food in the crop and gizzard. Since calcium chloride is very soluble, while the carbonate is insoluble, the chloride and carbonate contents have also been examined. The chloride content increased up to the first or second loop of the small intestine and then fell, while carbonate was absent in these two loops but reappeared further down the tract. In non-layers the solubility of calcium decreased from the anterior to the posterior ends of the small intestine, corresponding to a rise in *p*H, but this trend was not so noticeable in layers, possibly due to their increased retention.

When the faeces of laying birds were collected at eight-hourly intervals, it was found that heavy phosphorus excretion appeared about or shortly before the time of oviposition, *i.e.* corresponding to the time of most active shell-formation.

An examination of the blood showed that eggs were laid when blood calcium was either low or falling, but that shell thickness was not correlated with blood calcium. Similarly plasma phosphatase showed a closer correlation with productivity than with shell strength.

Bone salts and their mobilization

The greater part of the mineral matter in bone consists of tricalcium phosphate in physical association with calcium carbonate, *i.e.* bone salt is not a carbonato-apatite. The remainder of the mineral matter consists of calcium citrate, whose presence has been ascribed to co-precipitation with the other two minerals.

During the pre-laying period sufficient calcium is stored in the long bones to supply the shells for six eggs. This calcium is withdrawn during the first few weeks of egg laying, when the bird is in negative calcium balance, and if the bird does not cease laying is replaced later in the laying year. When a bird ceases production this calcium is excreted.

Egg shell formation

As the ovum passes down the oviduct it spends 18 minutes in the infundibulum, 3 hours in the magnum, 1 hour in the isthmus and 20–24 hours in the shell gland. The shell itself consists of two main layers, an inner mammillary layer, composed of calcite, but containing also magnesium compounds and phosphates, and an outer spongy layer of nearly pure calcite, the crystals being bound together by a matrix of collagen-like protein. The mammillary layer comprises about one-third of the shell and is laid down in the first ten hours. The spongy layer is then laid down in the remainder of the time. From four hours onwards, the amount of shell deposited can be calculated from the following formula:—

$$y = 5{\cdot}644x - 16{\cdot}617$$

where y = percentage of shell deposited, and x = hours in shell gland.

Sulphanilamide has been shown to inhibit the activity of carbonic anhydrase *in vitro.* When it was added to the diet the birds laid thin, pitted or shell-less eggs, and since blood calcium levels were unaffected, one may presume that these effects were due to the inhibition of the carbonic anhydrase activity of the shell-gland.

The shell gland has a *p*H of 6·2 and is therefore unlikely to secrete solid calcite; egg white (*p*H 8·2 to 9·2) could provide the necessary local alkalinity, secretion of egg shell then being brought about by the break-down of calcium proteinate and by carbonate ions liberated from bicarbonate by carbonic anhydrase. In this connexion it is noteworthy that manganese salts increased the activity of carbonic anhydrase *in vitro* and also caused stronger shelled eggs to be laid when included in the diet.

Shell characters

It has been shown that the percentage of shell in an egg was influenced by the shell thickness and the size of the egg, but not by its shape, and no significant difference in shell thickness was found with the position in the clutch.

While shell thickness to some extent is controlled genetically, *e.g.* lines laying thin-shelled and thick-shelled eggs have been established, diet also exerts a profound effect. On a diet low in calcium, egg shells became progressively thinner until they reached about 60 per cent of their normal thickness before egg production ceased, and in some instances shell-less eggs were laid.

The specific gravity of the egg is partially a function of shell thickness (the specific gravity of the shell of the hen's egg is about 2·3), and workers have attempted to relate it to hatchability. It was found that eggs whose specific gravities were less than 1·086 for White Leghorns or 1·078 for Barred Rocks showed reduced hatchability, but when the specific gravity was greater than these values, fertility was increased by 7·8 per cent and the hatchability of fertile eggs was increased by 32·4 per cent.

The flow of air or water through egg shells is slower outwards than inwards, indicating that in porosity measurements on egg shell the direction of flow must be stated. As with shell thickness, the porosity of the shell can be controlled genetically as well as by environment. Eggs from hens bred in areas of low relative humidity were found to have a low porosity, thereby reducing losses by evaporation and improving the keeping quality ; while in eggs from hens bred in areas of high humidity the porosity and hence the evaporative losses were higher and the eggs did not keep so well.

Studies with isotopic forms of calcium and phosphorus

When a single dose of isotopic calcium was administered about 50 per cent was excreted in the faeces in less than 48 hours, and 30 per cent was deposited in the shell of the egg laid one day after dosing. The excretion in yolk and albumen accounted for only 1 per cent. Continued dosing caused an equilibrium to be established in about 8 days.

Similar experiments using isotopic phosphorus showed that this was present in yolk, albumen and shell within 24 hours. The maximal recoveries were obtained in the shell in 24 hours, in the albumen in 48–72 hours but not until 6 days in the case of the yolk. Isotopic phosphorus was found in the tibia 40 days after dosing, indicating that phosphatic phosphorus is deposited in and removed from the skeleton during egg laying. It was also found that cholecalciferol aided the absorption of phosphorus from the intestine, and that the antiperotic water soluble vitamins (riboflavin, pantothenic acid, nicotinic acid, pyridoxine and folic acid) increased the deposition of phosphorus in bone. With continued dosage, phosphorus equilibrium was not achieved until 15 days, as compared to 8 days for calcium. This was probably because the metabolism of phosphorus into phospholipid and the deposition of the phospholipid in the developing yolks required the longer period.

MANGANESE

The importance of manganese in the prevention of perosis and its effect on shell strength are now fully appreciated, and these two aspects have attracted considerable attention.

Although perosis can be due to other causes, the general problem will be considered here.

Perosis

It was found that the presence of excessive amounts of calcium and phosphorus in the diet increased the manganese requirement, *i.e.* the excess calcium and phosphorus reduced the efficiency of absorption of manganese from the intestine.

Experiments *in vitro* showed that insoluble calcium phosphate, ferric citrate and steam bone meal removed manganese from solution by adsorption of the manganese whether or not food was present, and that gelatinous precipitates of dicalcium hydrogen phosphate removed more manganese than did crystalline precipitates. Organic constituents of the food could also remove manganese from solution, although oyster shell was ineffective in this respect if food was present.

In isolated loops of intestine absorption varied with the concentration, between 28 and 44 per cent being absorbed in 2 hours, and the rate of absorption was not markedly affected by the presence of normal amounts of calcium and phosphorus.

It has been suggested that the amount of manganese soluble in 0·1N HCl was a good guide to the value of the diet in preventing perosis, provided due regard to the levels of calcium and phosphorus was observed. With normal levels of calcium and phosphorus 3 p.p.m. of HCl-soluble manganese prevented perosis, but high levels of calcium and phosphorus increased the requirement.

It is known that manganese increases the activity of phosphatases, while calcium and phosphorus depress it, and it was found that both blood and bone phosphatase activities were lowered when the bird developed perosis.

In addition to manganese, several other factors are necessary to prevent perosis, and of these possibly choline is the most important. When the perosis score was plotted against the percentage of total choline in the diet it was found to decrease as the choline content increased, reaching a minimal value at 0·19 per cent choline. Betaine and methionine could each assume a certain portion of choline function in the chick but could not replace choline for the prevention of perosis. Arseno-choline, however, could do so and since the effects of these three compounds were additive, together they were equivalent to choline.

Laying hens

When laying hens were fed a diet low in manganese, embryonic deaths in their eggs occurred at 18–21 days, and those chicks not breaking the shell contained less manganese than those chicks that succeeded. Increasing the level in the diet caused an increase in egg content, but did not affect fertility. Moreover, second year hens needed more manganese in the diet for egg production, maintenance of shell quality and hatchability than did first year pullets.

Finally, an interrelation between manganese and vitamin D has been demonstrated; sunlight, ultra-violet light or vitamin D reducing the dietary demand for manganese.

SODIUM CHLORIDE

Much of the research on sodium chloride has been directed towards the amounts necessary to cause death. When 4 g. salt per Kg. live-weight was placed in the crop it proved toxic, but the same amount was non-toxic when mixed with the food.

Adult birds tolerated higher concentrations of salt in the diet than did young chicks. Adult stock have been fed 20 per cent salt for 4 weeks without mortality and at 30 per cent only a few deaths were reported. Birds two to three months old withstood levels of 5, 10 and 15 per cent with only a slight mortality, yet 5 or 10 per cent caused heavy mortality when fed to baby chicks.

Additions of salt to the drinking water were not tolerated by baby chicks, and levels of 0·9 to 2·0 per cent caused 100 per cent mortality.

During the first month after hatching both the water and the salt contents of skin and muscle increase rapidly.

Salt improves the utilization of dietary nitrogen. The addition of 0·5 per cent salt to an otherwise salt-free diet increased the average daily balance of nitrogen in laying hens from – 0·4 to + 4·4 grammes and the average percentage retention from 22·5 to 37·0.

IRON AND COPPER

The iron and copper contents of eggs were higher in spring than in winter, and feeding additional iron salts depressed the copper content. Freshly laid eggs contained all their iron (about 1 mg. per egg) in the yolk. During storage some iron passed from the yolk to the albumen, but the amount was so small that it had little effect on the yolk content.

Both iron and copper interfered with the absorption of manganese. Manganese and iron increased the egg production of birds fed indoors, but not those fed outdoors, and copper improved the hatchability when added to the diets of both indoor and outdoor birds.

When the egg is incubated there is a gradual transference of iron into the living tissue, where it is largely converted into haem for the synthesis of haemoglobin. During the first fortnight most of the haemoglobin is in the membranes, a fact which presumably reflects the richness of the circulation of these structures. Only at the fifteenth day does the embryo body attain parity with the membranes in this respect, but later in the incubation period there is a steep and spectacular fall in both the proportion and absolute quantity of haemoglobin in the membranes, until at hatching almost the whole of the haemoglobin which has been synthesized (equivalent to 0·7 to 0·8 mg. Fe) is concentrated in the embryo body.

DELETERIOUS MINERALS

SELENIUM

Laying hens could tolerate 2·5 p.p.m. selenium without exhibiting any ill effects in egg production, fertility or hatchability. Five p.p.m. caused a reduction in hatchability and 10 p.p.m. reduced hatchability to zero, although egg production and fertility were unaffected, and food consumption did not decrease. The toxic effects of 10 p.p.m. selenium could be partly counteracted by the addition of 5 p.p.m. arsenic to the drinking water.

Poultry reared for meat or eggs produced on diets containing 2·5 p.p.m. selenium were not harmful to humans, but at 10 p.p.m. were adjudged unsafe.

MOLYBDENUM

The addition of molybdenum to the diet depressed the growth rate, but 400 p.p.m. were not fatal. An increase in dietary molybdenum was accompanied by an increase in blood molybdenum, which could be reduced by the addition of copper to the diet. The author of the paper suggested that, since most of the molybdenum in the plant was in the foliage, molybdenum toxicity in poultry was unlikely. It is difficult to reconcile this view with the widespread use of dried grass meal and dried alfalfa meal in poultry diets.

VITAMIN REQUIREMENTS AND METABOLISM

The requirement of the fowl for a particular vitamin, especially for one of those in the vitamin B complex, cannot be assessed accurately since it depends on the environmental conditions, the type of diet eaten and the rate of growth.

The microflora of the intestine are capable of synthesizing a number of vitamins, and these may become available to the host, thereby reducing the demand from the food. Other foods contain antivitamins, whose presence increases the requirement by destroying or inhibiting or otherwise rendering part or all of a vitamin unavailable to the bird.

A constituent of the diet may increase or decrease the requirement: a diet high in carbohydrate increases the requirement for thiamine, whereas a diet low in carbohydrate and high in fat, although supplying the same amount of available energy to the bird, reduces the demand for thiamine. An imbalance of the vitamins may lead to trouble, for instance, an excess of thiamine may cause symptoms typical of pyridoxine deficiency.

The requirements for some vitamins are affected by the amino-acid composition of the diet, *e.g.* methionine exerts a sparing action on pantothenic acid and tryptophane for nicotinic acid.

Finally, there is evidence that heavy breeds have higher requirements for growth than light breeds.

The figures given in Table 3.12, are the allowances recommended for poultry by the National Research Council of the U.S.A. The sub-committee of this council examined the evidence for requirement values; since the list of publications at the end of the report relates to U.S.A. work it must be presumed that only U.S.A. work was considered. To the requirement value agreed upon by the committee a margin of safety was added to allow for variations of content of the individual meals and destruction in the mash, as well as the points mentioned above, and the final value is given as the nutrient ‘ allowance ’. It is therefore clear that diets containing these allowances will not necessarily be fully adequate for poultry under all conditions, but nevertheless are a very valuable guide in the compounding of poultry feeding stuffs.

TABLE 3.12

VITAMIN REQUIREMENTS OF POULTRY

	Chicks (0–8 wks)	*Growers (8–18 wks)*	*Laying hens*	*Breeding hens*
Vitamin A activity (i.u./g.)	44	44	73	73
Vitamin D (i.u./g.)	6·1	6·1	15·5	15·5
Biotin (μg./g.)	0·099	?	?	0·154
Choline (μg./g.)	1540	?	?	?
Folic acid (μg./g.)	0·77	?	?	?
Nicotinic acid (μg./g.)	17·6	?	?	?
Pantothenic acid (μg./g.)	11·0	11·0	5·5	11·0
Pyridoxine (μg./g.)	3·5	?	3·5	3·5
Riboflavin (μg./g.)	3·5	2·0	2·0	2·9
Thiamine (μg./g.)	2·0	?	?	?
Vitamin K_1 (μg./g.)	0·40	?	?	?

In the account given below the typical symptoms of the vitamin deficiency follow the other information relating to that particular vitamin. It must be borne in mind, however, that these symptoms were produced by feeding diets deficient in one vitamin only, and moreover, are symptoms of an acute deficiency. In the field it is rather rare to find that a diet completely devoid of any one particular vitamin has been fed. Most cases relate to the partial deficiency of one or more vitamins, thus making diagnosis much more difficult.

VITAMIN A

In 1950 crystalline vitamin A acetate was adopted as the standard for vitamin A by the Expert Committee on Biological Standardization of the World Health Organization. The International Unit is 0·344 μg. and this has the same potency for the rat as the old standard of 0·6 μg., of β-carotene. It has been shown that wide variations in the storage of vitamin A in the livers of both the chick and the rat can be caused by the diluent and that the storage of vitamin A in chick livers from 130 μg. of β-carotene is markedly reduced by 100–300 μg. of Xanthophylls. Liver storage is increased by the addition to the diet of vitamin E, methylene blue, thiodiphenylamine or Antabuse in the presence of cod-liver oil but not when the cod-liver oil is replaced by lard. Moreover, β-carotene in oil is less efficiently utilized than is β-carotene in lucerne, which again is less efficient than fish-liver oil; it was also shown that while vitamin A was superior in building liver reserves, carotene from lucerne was superior in the transfer of vitamin A and carotene to the egg.

When vitamin A-deficient chicks were dosed with β-carotene, vitamin A was found in the intestinal wall ½ hr. later, and an increase in the liver 3½ hr. later indicating that, as in the rat, the conversion of carotene to vitamin A takes place in the intestinal wall and not in the liver.

An attack of coccidiosis severely erodes the intestinal wall, and birds so infected and fed β-carotene showed much lower liver storage than similar birds fed an equivalent amount of vitamin A, thus further supporting the view that β-carotene is converted into vitamin A by the intestine.

Cryptoxanthin was about half as potent as β-carotene, and was therefore comparable with α and γ carotenes.

Newly hatched chicks contained about 40 to 50 i.u. of vitamin A. On a vitamin A deficient diet, this decreased rapidly and might be exhausted in less than 2 weeks. When the diet was adequately supplied with the vitamin, liver storage increased, as is seen by the results set out in Table 3.13.

Laying hens do not normally have a large reserve of vitamin A, the average concentration in the liver being 370 i.u. and when the level in the blood plasma drops below 50 i.u. per 100 ml. the body reserves are depleted. The requirement for good egg production seems to be either the same or greater than that for good hatchability.

TABLE 3.13

EFFECT OF DIETARY VITAMIN A LEVELS ON LIVER CONTENT

Vitamin A Potency of diet (μg./100g.)	*Vitamin A Potency of liver after 3 wks* (*i.u.*)
250	116
500	270
750	541
1000	212
1500	712
2000	368

The pigments present in the yolk of the egg have been divided into vitamin A 280 i.u., Xanthophylls 1497 μg., β-carotene 49·2 μg., spurious carotene 35·8 μg., and cryptoxanthin none. It has also been shown that 'green yolks' are caused by a pigment identical with that obtained by the acid treatment of carotenoid pigments.

Deficiency symptoms

On a severely-deficient diet the symptoms begin to appear at about 20 days old. The growth-rate is reduced and the chicks are weak and emaciated with ruffled plumage and a staggering gait. Mortality is usually high and their resistance to infection is decreased. The third eyelid may become keratinized, and the salivary, tear, and intestinal mucous glands cease to function.

Post-mortem examination reveals creamy white pustules on the roof of the mouth and along the oesophagus. Urates accumulate in the ureters and in the kidney tubules causing them to be distended and creamy-white in colour.

In mature birds the symptoms develop more slowly, but the eye disorder often becomes more acute and egg production and hatchability are markedly reduced.

CHOLECALCIFEROL (VITAMIN D_3)

Vitamin D occurs in two forms, ergocalciferol and cholecalciferol, of which the latter is about 50 times as potent for chicks as the former, although both are equally effective for rats. At a meeting in 1949 of the sub-committee on fat soluble vitamins, crystalline cholecalciferol, used as standard by the British Standards Institution was adopted as the International Standard; one i.u. is the potency of 0·025 μg. of this compound and is equal to one B.S.I. unit. The Association of Official

Agricultural Chemists of U.S.A. unit, previously adopted by the U.S.A. has been compared with the international unit and it was found that one i.u. is equal to 1·3 A.O.A.C. units.

Cholecalciferol is relatively stable, about 37 per cent of the activity was lost in the first 15 weeks, and 73 per cent in 120 weeks when stored as cod-liver oil. The rate of destruction was reduced to negligible amounts by admixture with soya bean meal or cereal products, but when mixed with fuller's earth or kaolin all activity was lost in 4 weeks.

The minimal requirement of the chick for cholecalciferol depends not only on the level of vitamin in the diet, but also on the amounts of calcium and phosphorus present and on the Ca : P ratio. The potency of the vitamin preparation can be measured by growth, degree of calcification of the tibia or the toe, the healing of rickets or the measurement of the tarso-metatarsal distance and it has been shown that of these the ash content of the tibia or toe and the tarso-metatarsal distance are equally reliable criteria.

The fowl is capable of synthesizing cholecalciferol on exposure to sunlight or irradiation to ultra-violet light. It is known that the natural vitamin precursor is 7-dehydrocholesterol and with ultra-violet light the band between 200 and 280 mμ seems to be the most effective. Earlier workers have shown that most of the vitamin D in egg yolk is present as a precursor.

Deficiency symptoms

The typical symptom of a deficiency of vitamin D is the lack of proper calcification, resulting in rickets. The bones and beak become soft and rubbery, and beads develop at the ends of the ribs. The toes spread out, growth is retarded and the legs may become bowed.

In mature birds the same symptoms are observed, and in addition the eggs become thin-shelled, followed by reduced egg production. Hatchability is reduced and egg production may cease.

These symptoms are also seen when calcium or phosphorus is deficient, but in the field are more frequently due to vitamin D deficiency.

VITAMIN E

The protein : carbohydrate ratio, the dietary content of unsaturated fatty acids, the proportion and nature of the salts present (especially common salt) and the presence or absence of lipotropic substances have all been shown to have an influence on the manifestation of symptoms of avitaminosis E in the chick, and the relative incidence of the two principal syndromes is determined by the nature of the predisposing causes other than the simple deficiency of vitamin E.

Purified diets that did not contain fat were reported rarely to produce exudative diathesis and never to produce encephalomalacia. Fresh and partly rancidified oil were both equally effective in producing the symptoms, while completely rancidified oil did not. High salt concentrations in the diet were conducive to the production of exudative diathesis. Inositol prevented both encephalomalacia and exudative diathesis, lipocaic prevented exudation and cholesterol prevented encephalomalacia but favoured the production of exudates.

It has been suggested that the utilization of vitamin A depends to some degree on the presence of vitamin E and an A-E synergism has been demonstrated, so it may well be that the above observations all relate to the destruction of vitamin E in the alimentary canal and (in part) to the effects of such destruction on vitamin A metabolism.

The three forms of vitamin E are not equally effective for the fowl, α-tocopherol being four times more potent than β-tocopherol and ten times that of γ-tocopherol. The allowances suggested by the rather meagre literature are 1·0 μg. of natural vitamin E per g. live-weight per day for chicks and 1·2 mg. of α-tocopherol per day for laying hens.

Deficiency symptoms

Two syndromes are associated with a deficiency of vitamin E and these may be seen separately or together. In one, exudative diathesis, the skin becomes a strawberry colour, particularly under the wings. An oedema is noted under the skin and this exudate is frequently found in the pericardial cavity. The other, nutritional encephalomalacia, results in the chicks being ataxic and unable to walk or stand. When attempts are made to walk or stand the chick falls over, usually backwards, and paddles with its legs. In the earlier stages the chick reels about as if drunk, falls over and paddles and then appears to recover for a while before repeating the performance. Post-mortem examination reveals lesions in the cerebellum, which is often greatly enlarged.

In mature fowls egg production is not greatly affected but hatchabilty is markedly reduced. Most embryonic deaths occur at about the third or fourth day as a result of a circulatory failure and the walls of the blood vessels are easily ruptured.

VITAMIN K

Two naturally occurring vitamins K have been isolated, one K_1 from alfalfa and the other K_2 from putrefied sardine meal. In addition 2-methyl-1 : 4 naphthaquinone (vitamin K_3) has twice the activity for chicks of vitamin K_1 and three times that of vitamin K_2. Vitamin K is unstable to alkalis and is photolabile; over 75 per cent of vitamins K_1 or K_2 were destroyed in 5 hrs exposure to sunlight.

The vitamin is present in egg yolk, but not in egg albumen, and only small amounts were found in the tissues of young chicks.

Deficiency symptoms

A deficiency of vitamin K results in the prolongation of the clotting time of the blood, so that chicks fed diets deficient in vitamin K may bleed to death from an injury or bruise.

Mature birds do not seem to exhibit these symptoms, but chicks hatched from their eggs are deficient in the vitamin and may bleed to death from an injury, such as wing banding.

BIOTIN

The carbohydrate portion of the diet has a profound effect on the results when hens are deprived of biotin. Dextrin favoured intestinal synthesis of biotin, thereby greatly reducing the severity of the deficiency, on the other hand, sucrose did not favour this synthesis, nor did lactose or dried whey. It was also shown that when eggs contained 0·15 μg. biotin per g., normal embryonic development took place; eggs from hens on normal diets contained 0·065 to 0·105 μg./g. in the albumen and 0·5 μg./g. in the yolk. These contents were not affected by the inclusion of unsaturated fats in the diet. A deficiency of biotin in the maternal diet did not reduce the number of eggs laid but seriously affected the hatchability.

Egg albumen contains a compound, avidin, which has the power of combining with biotin to render it biologically inactive. Experiments using radio-active biotin showed that 23·8 μg. biotin combined with 3·25 mg. avidin, giving a probable formula for the compound of AB_2, which showed only slight dissociation (0·08 per cent).

It has been reported that L-biotin and DL-allobiotin had no activity, and that oxybiotin prevented the appearance of the deficiency symptoms but did not permit maximal growth. From 3–5 μg. of oxybiotin gave the same response as 1 μg. biotin. Biotin and oxybiotin were not converted into each other by the bird and the sulphur atom did not seem to be essential for biological activity.

Deficiency symptoms

The lesions observed when chicks are reared on a biotin deficient diet may be confused with those seen when the diet is deficient in pantothenic acid. The two deficiencies can be distinguished by observing the order of incidence of the lesions. In biotin deficient chicks the crusty scabs first appear on the feet, while in pantothenic acid deficiency the scabs are first noticed on the head, usually at the corners of the mouth. Biotin has also been reported as one of the factors involved in perosis-prevention.

Adult stock do not exhibit the lesions, but hatchability is reduced.

CHOLINE

Choline performs many functions in the body, such as tissue and lipid synthesis, lipotropic action, methylating action, and perosis prevention, and although choline can be replaced by compounds such as betaine and methionine for some functions, no single compound has yet been found that can replace it for all functions. Excessive amounts are mildly toxic, *e.g.* while 1 per cent gave good growth, 4 per cent caused growth retardation.

During incubation the accumulation of various known methylated compounds accounted for less than 10 per cent of the choline metabolized, and it has been suggested that some of this was transformed into glycine.

The function of choline as a methylating agent is discussed under cobalamin.

Deficiency symptoms

A diet deficient in choline causes reduced growth and perosis, and excessive amounts also cause reduced growth.

The available evidence suggests that mature birds can synthesize sufficient choline to meet their requirements for egg production and hatchability.

FOLIC ACID

Because of its importance in anaemia, folic acid has been intensively studied, although the vitamin was not isolated in the crystalline form until 1941. Some confusion over the vitamin was sorted out when it was found to exist in three forms, pteroylglutamic acid, pteroyltriglutamic acid and pteroylheptaglutamic acid, all of which possessed the same activity for the chick but differed in their activities for the microflora used in the microbiological assays. Folinic acid was equal to folic acid for the chick, pteroic acid was active for the microflora but inactive for the chick, and a further compound, pteroylamino-pimelic acid also had folic acid activity for the chick. Para-aminobenzoic acid can be utilized by the intestinal flora to synthesize folic acid, which then becomes available to the host ; and the citrovorum factor is a derivative of folic acid.

Other substances act as folic acid inhibitors, *e.g.* pteroylaspartic acid and 4-amino-pteroylaspartic acid, while the corresponding glutamic acid conjugates possess greater inhibiting power.

The concentration in chick muscle does not appear to be affected by the dietary level, but liver levels can be increased fifteen times by dietary means, although it must be remembered that the assay methods are as yet somewhat suspect due to the existence of the conjugates with glutamic acid. The vitamin has an effect on methionine metabolism ; liver tissue from depleted chicks had a lowered power of forming this amino-acid from homocystine or homocysteine and choline or betaine. It was also partially destroyed by heat, the content in low temperature dried herring meal was 4·1 μg./g. while normal commercial drying reduced this to 0·3 μg./g.

Deficiency symptoms

Folic acid deficiency in young chicks is accompanied by retarded growth, poor feathering and feather depigmentation. These symptoms are additional to the development of an anaemia characterized by a reduction in the number of red blood cells, which, however, are increased in size, abnormally shaped and less fragile than normal.

NICOTINIC ACID

While chicks can synthesize nicotinic acid from tryptophane the rate of synthesis is usually too slow to allow the chicks to exhibit maximal growth, and it must be considered an essential vitamin for the chick. Much of the nicotinic acid in cereal products is present as a precursor, which is not available to the chick, and an inhibiting effect on growth is noted if maize grits are added to an otherwise satisfactory synthetic diet containing suboptimal amounts of nicotinic acid. This inhibiting effect can be counteracted by adding nicotinic acid to the diet. Most practical diets, however, are adequately supplied with the vitamin to permit maximal growth, although the ' High Energy Diets ' used in broiler feeding in U.S.A. and containing about 80 per cent maize, are often supplemented with pure vitamin, since maize is very low in available tryptophane.

Requirement values have all been determined using synthetic diets, the criteria being growth and the prevention of perosis.

Deficiency symptoms

Diets deficient in nicotinic acid cause ' black tongue ' when fed to chicks, when the entire mouth cavity in addition to the upper part of the oesophagus becomes inflamed a deep-red colour.

PANTOTHENIC ACID

Experiments to ascertain pantothenic acid requirements are usually carried out using natural meals subjected to dry heat to destroy the pantothenic acid, and some workers have concluded that the level in the liver is a less satisfactory criterion of deficiency in chicks than is growth. Pantothenol also has pantothenic acid activity and was about 90 per cent as active. Livers from chicks fed diets deficient in cobalamin contained more pantothenic acid than did those fed adequate diets. The level in the egg reflected the level in the diet. During storage, pantothenic acid was transferred from the yolk to the albumen as illustrated in Table 3.14.

TABLE 3.14

PANTOTHENIC ACID CONTENTS OF FRESH AND STORED EGGS

	Fresh eggs		*After 1 yr. storage*	
	μg./g.	*Total*	*μg./g.*	*Total*
Yolk	30·6	511	17·8	347
Albumen	3·0	98	7·8	213
		609		560

Deficiency symptoms

Pantothenic acid deficient diets cause a dermatitis somewhat similar to that caused by a biotin deficiency, but the lesions are first seen at the corners of the mouth and eyes and only in extreme cases do the lesions on the feet become really severe.

Lesions have not been reported for mature birds although hatchability is reduced.

PYRIDOXINE

Diets compounded of ordinary feeding stuffs contain an abundance of pyridoxine for maximal growth, and hence the vitamin has not yet been intensely studied. It is known that at least three substances have vitamin B_6 activity; pyridoxine, pyridoxal and pyridoxamine, the relative efficiencies being in the ratio 1 : 0·5 : 0·8 respectively.

Deficiency symptoms

Pyridoxine deficient diets support little or no growth in chicks, which become extremely jerky in their movements. Convulsions may occur similar to those seen in vitamin E deficiency and the head may be retracted over the back. The convulsions are followed by a period of complete exhaustion.

In mature birds a deficiency is characterized by anorexia, followed by a rapid loss of weight and death. Both egg production and hatchability are markedly reduced.

RIBOFLAVIN

Most of the commoner poultry foods are low in this vitamin, and rich sources are expensive; the requirements for good growth of chicks and good hatchability have therefore been the subject of many investigations. Most workers on chicks have used growth and the prevention of curled toe paralysis as their criteria of adequacy, although tissue saturation has been suggested as providing a more satisfactory criterion of maximal well-being.

Tissues from chicks adequately supplied with riboflavin contained about one and a half times as much as did those deficient in the vitamin, and muscles were more retentive of their store of riboflavin than were liver, kidney or heart. Retention of nitrogen was also reduced when the diet was deficient in riboflavin.

No change was detected during incubation in the amount of riboflavin in the egg and the level in the hen's diet was correlated with the amount in the tissues of the chicks from her eggs, and with the levels in the blood serum and the egg. Of the three naturally occurring forms, free vitamin, flavin-mononucleotide and flavin-adenine-dinucleotide, the free vitamin forms by far the greater part of that in the blood serum of laying hens and of both yolk and albumen of the egg, while, still with the exception of the magnum section of the oviduct, that in the tissues is nearly all in the combined form, whether the diet be deficient or adequate. It has been suggested that in laying hens, any combined riboflavin in the food is de-phosphorylated by the intestinal wall, and passes into the blood as free vitamin. It accumulates, in the magnum, still as the free vitamin, during the intervals between the passage of eggs. When the egg passes down the magnum the riboflavin and albumen are secreted simultaneously.

When the dietary level is changed about eight days elapse before the egg level becomes constant again. Between 24 and 30 per cent of the dietary riboflavin is recovered in the egg and maximal storage is observed when the diet contains 5·0 μg./g. although maximal hatchability can be obtained from diets containing 3·6 μg./g. Riboflavin is found in both a higher concentration and in a slightly higher total amount in yolk than in albumen in most eggs, although in about one quarter of the eggs the albumen contains more total riboflavin than does the yolk. Birds have been selected for resistance and susceptibility to dietary deficiencies in riboflavin.

Deficiency symptoms

Chicks reared on a diet devoid of riboflavin, or containing only very low levels grow at an extremely slow rate. A slight increase in the riboflavin content of the diet greatly increases the growth rate, although this still remains poor. After two or three weeks on this somewhat less deficient diet birds can be seen walking on their hocks, with the toes curled up like a fist, the typical symptoms of ‘ curled toe paralysis ’. Post-mortem examination at this stage shows that the brachial and sciatic nerves are greatly enlarged and may be four or five times their normal size. Since the requirement decreases with increasing age, chicks frequently recover from the symptoms even though the diet is not changed.

In breeding hens a deficiency results in decreased hatchability, a peak in embryonic mortality develops at about the twelfth day, while in many of those which survive till the twentieth day the down follicle fails to rupture, giving the characteristic ‘ clubbed down ’ condition which is mainly seen in the ‘ dead-in-shell ’ chicks.

THIAMINE

Thiamine pyrophosphate is the prosthetic group of the co-enzyme co-carboxylase, and much of the work on the vitamin has been directed to the study of the enzyme. In polyneuritic chicks the amount of co-enzyme available for the metabolism of pyruvic acid is reduced, and *in vitro* a depression of the utilization of pyruvic acid by cardiac muscle from ducks deprived of thiamine has been reported.

Thiamine deficient animals usually exhibit anorexia, but by force-feeding to avoid this, pigeons previously starved to deplete fat and thiamine stores showed no impairment of fat synthesis from thiamine-free carbohydrate. It has also been noted that pigeons on a thiamine-deficient diet became increasingly resistant to the convulsive action of camphor as the deficiency progressed, and the influence of the avitaminosis on the detoxification of camphor has been raised.

Differences in the efficiency of transfer of thiamine to the egg exist between breeds, White Leghorns being more efficient in this respect than Plymouth Rocks or Rhode Island Reds. All the thiamine is originally deposited in the yolk and it was suggested that the hen can transfer more thiamine to the egg at the beginning of the laying season than at the end. This group of workers also stated that nearly all the thiamine disappeared during incubation, although others reported that the total content did not vary, the decrease in the egg being balanced by the increasing amounts found in the embryo. The level of thiamine in the blood was not increased by oestrogen administration: in this respect it differed from riboflavin, calcium and many other blood constituents.

Deficiency symptoms

When chicks are reared on a thiamine-deficient diet they exhibit anorexia, emaciation and occasionally convulsions. After about ten days they develop polyneuritis and in the acute stages the head is drawn over the back.

Hatchability does not seem to be affected, but the newly hatched chicks rapidly develop polyneuritis and they rarely survive the first day.

THE ANIMAL PROTEIN FACTOR AND COBALAMIN

The existence of the Anti-Pernicious Anaemia Factor was first suspected some 25 years ago, for in 1926 it was found that pernicious anaemia responded to the oral administration of large amounts of liver.

It was also well-known that protein of animal origin was necessary in the diet to secure good growth in chicks and good hatchability in the eggs of breeding hens. Even when the contents of all the known vitamins and the amino-acids were equalized, animal protein was still superior to vegetable protein, and the name 'Animal Protein Factor' (A.P.F.) was coined to give verbal expression to this superiority. In experiments necessitating the use of highly-purified diets, liver extracts were added to supply this factor.

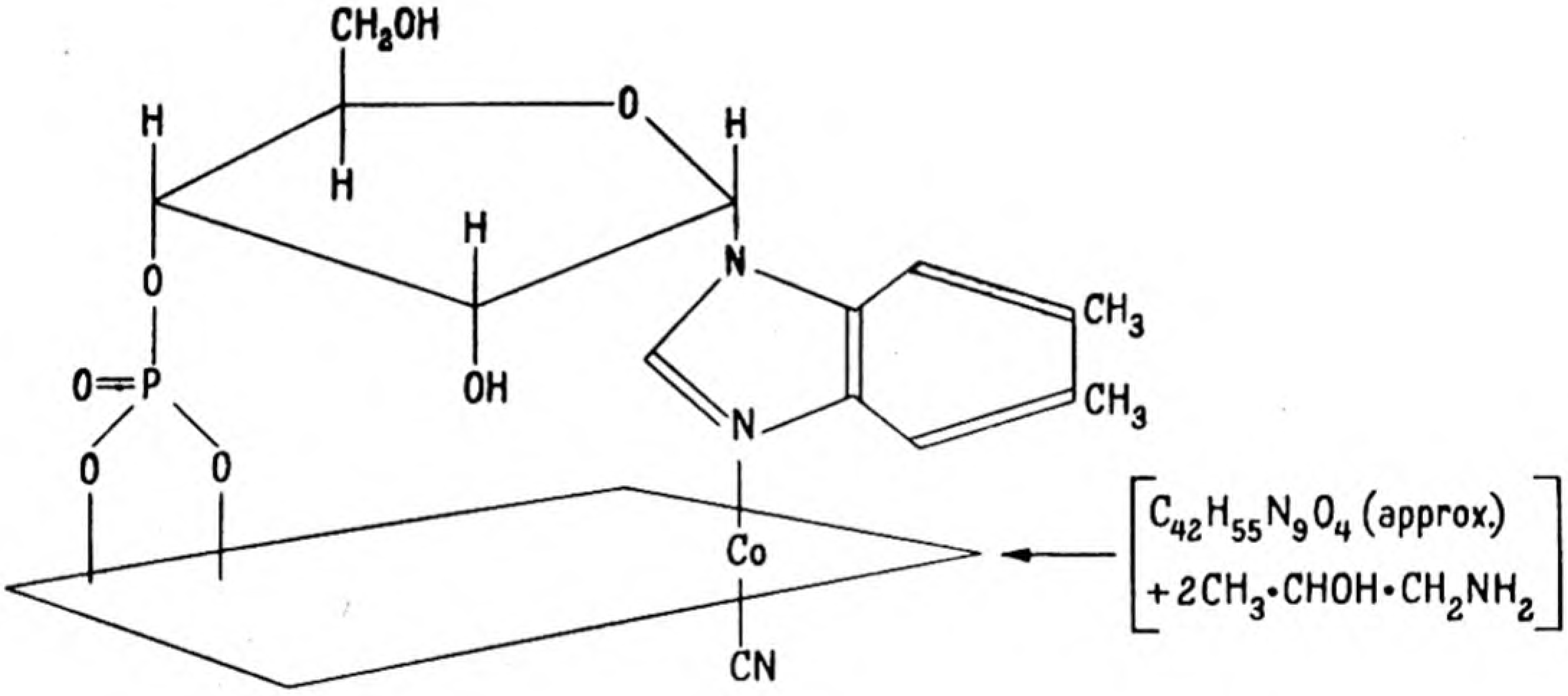
In 1948 the isolation of the anti-pernicious anaemia factor was reported from U.S.A., followed a week later by its independent isolation in the United Kingdom. Comparison of the two factors showed that they were identical. Since then it has been shown that a number of compounds of closely similar chemical constitution possess anti-pernicious anaemia activity. The generic name 'Cobalamin' has been adopted for the whole group by the International Union of Pure and Applied Chemistry, and the old nomenclature of vitamin B_{12} has been abandoned.

Cobalamin contains one atom of cobalt per molecule and the various cobalamins differ from each other only in the radical satisfying one of the cobalt valencies. This may be cyanide, hydroxide, etc., giving cyanocobalamin, hydroxocobalamin, etc.

Since liver extracts were a potent source of A.P.F., it was at first thought that cobalamin was A.P.F. Further work has shown that, although cobalamin possesses many of the properties of A.P.F. and probably is the major component, A.P.F. comprises at least two as yet unknown substances.

Cobalamin has a molecular weight of about 1300 and crystallizes in deep-red crystals of the orthorhombic system, which blacken without melting at 300°C.

The following partial formula has been suggested.



The portion represented as a plane contains the cobalt atom and is thought to be roughly planar in nature. It is resistant to both acid and alkaline hydrolysis; and while the products of degradation have been studied, the evidence obtained is inconclusive.

Factors closely related to cobalamin

Comparison of assay methods using different micro-organisms and chicks showed that rumen contents and calf dung contained substances closely resembling cobalamin in their chemical and physical properties, but differing biologically. These have been isolated and resolved into four factors; pseudo-ψ-cobalamin and Factors A, B and C. Factor A showed slight activity for chicks, the others were inactive.

However, when these factors and cobalamin were passed through E. Coli, cobalamin was partially transformed into Factor A, and Factor B was transformed into a mixture of cobalamin and Factor C.

It is obvious that a very close link exists between these five substances, and work on bacteria may well help in the elucidation of some of the problems in poultry metabolism.

Requirements

The cobalamin requirement of the chick depends on the amount in the egg and this in turn is determined by the maternal diet. Table 3.15 indicates the relation between the level of cobalamin in the maternal diet and the requirement of the chick.

TABLE 3.15

RELATION BETWEEN MATERNAL DIET AND CHICK REQUIREMENT

	Maternal diet	*Chick requirement*
Cobalamin as μg./Kg.	0	27
	4	12
	8	3
	16	0

When breeding hens are maintained on diets capable of sustaining maximal hatchability the chick requirement is between 4 and 6 μg. per Kg. food, with the carry-over effect from the maternal diet lasting for about four weeks after hatching. The requirement increases with increasing levels of vegetable protein in the diet, suggesting that cobalamin is involved in protein metabolism.

Cobalamin is necessary for optimal hatchability. On a diet devoid of cobalamin hatchability fell to 20 per cent of the fertile eggs set after three months, yet remained at 80 per cent on a similar diet supplemented with fish meal. When the deficient diet was supplemented with pure cobalamin hatchability was maintained for nine to ten weeks and then began to decline, suggesting that the other factors known to be present in A.P.F. had then been depleted.

Egg production is not affected by feeding diets which do not contain animal protein, and it must be concluded that the dietary requirement for egg production is either nil or is extremely low.

Sources of A.P.F. and cobalamin

As has already been mentioned, A.P.F. is found in protein foods of animal origin but is absent from foods of vegetable origin. Before the isolation of cobalamin it had been found that dried cow manure could replace animal protein, provided it was treated to destroy its androgenic potency, although later work has suggested that this latter originates in the urine and not in the faeces.

An organism was isolated from poultry excreta which possessed the power to synthesize cobalamin. This power was evidenced in the analysis of litter of varying ages. Fresh litter contained only 0·001 μg.

cobalamin per g. dry litter; after one week this content had increased to 0·110 μg./g., and at the end of a year to 0·261 μg./g. These results indicate why it is possible to maintain good growth and hatchability on all-vegetable diets when the birds are housed on deep or built-up litter.

The cobalamin contents of some poultry feeding-stuffs are set out in Table 3.16.

TABLE 3.16

COBALAMIN CONTENTS OF POULTRY FEEDING-STUFFS

Feeding-stuff	*Cobalamin content mμg./g.*	*Feeding-stuff*	*Cobalamin content mμg./g.*
Red fish meal	62	Wheat	1
Sardine meal	154	Maize	0
Herring meal	260	Oats	3
White fish meal	95	Soya bean meal	2
Meat meal	36	Alfalfa meal	3
Liver meal	310	Dried yeast	1
Crude casein	104		

Cobalamin metabolism

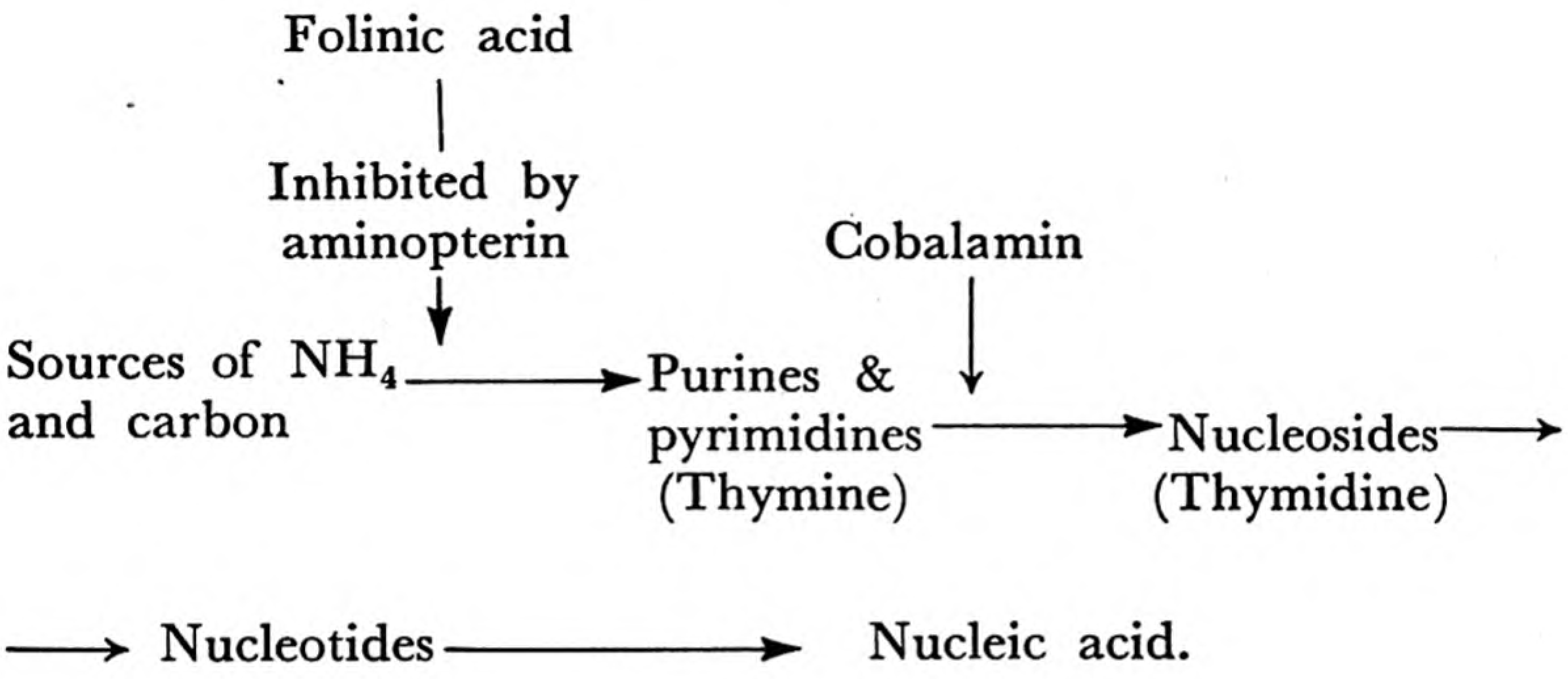
The addition of cobalamin to an all-vegetable diet increased the cobalamin content of the liver about five-fold and that of the kidney about twice, but that of the spleen was not affected.

Cobalamin plays an important role in transmethylation. It appears to be necessary for the transformation of homocystine to methionine, and the need for supplementary methylating compounds, *e.g.* choline or betaine, in the diet of chicks is directly influenced by the cobalamin content. Betaine seems to be more efficiently utilized by chicks with sub-optimal reserves of cobalamin than is choline.

It also counteracts glycine toxicity in chicks, and while 4 per cent glycine added to the diet caused a high mortality when the diet was deficient in cobalamin, the mortality was negligible when cobalamin was added.

The symptoms of folic acid deficiency were accentuated by the administration of cobalamin given either orally or by injection. Both ascorbic acid and cobalamin stimulated growth on a semi-purified diet whether or not folic acid was included in the diet. The inclusion of both ascorbic acid and cobalamin gave a greater increase in growth than did either alone, and both stimulated the synthesis of folic acid, as was shown by the increased storage of liver folic acid. The inclusion of folic acid in the diet stimulated the synthesis of cobalamin when this was omitted, but the effect of ascorbic acid was doubtful. The hypothesis has been put forward that cobalamin plays some role in the conversion of folic acid to the citrovorum factor, and that it may act either *in toto* or after alteration, as a co-enzyme for this reaction. It has also been suggested that cobalamin facilitates the absorption of folic acid and *vice versa*.

Another school has put forward the view that folinic acid is the ' biologically active ' form of folic acid, and has suggested the following interrelationship between the factors:



Pantothenic acid also exerted a sparing action on the requirement for cobalamin, and the converse was true.

GROWTH PROMOTING FACTORS

Once cobalamin had been isolated and was available in a pure form, a search was instituted for sources of supply other than liver. Of the many possible sources tested, the residues from the manufacture of antibiotics (*e.g.* aureomycin, streptomycin, etc.) proved to be amongst the richest. When these residues and a liver extract were fed in diets of equal cobalamin content, the chicks receiving their cobalamin from the residues grew more rapidly than those fed the liver extract. Further work showed that this increased growth was due to the small amount of antibiotic left in the residues after manufacture.

Subsequently it has been found that other dietary non-essentials can promote growth, *e.g.* surface-active agents and some organic arsenical compounds.

ANTIBIOTICS

The results set out in Table 3.17 show that when an all-vegetable diet was supplemented with either cobalamin or antibiotic the rate of growth was increased. Feeding both gave a further increase in live-weight gain and the combination of the two had the same effect as the addition of the antibiotic residues.

TABLE 3.17

EFFECT OF COBALAMIN AND ANTIBIOTICS ON LIVE-WEIGHT INCREASE

Supplement	*Average gain 2 to 4 weeks (g.)*	*Average gain as % gain on Basal diet*
None (Basal diet)	67·5	—
Cobalamin	128	190
Antibiotic	90	133
Cobalamin and antibiotic	135	201
Antibiotic residues	133	197

The antibiotic group of drugs now comprises a large number of different therapeutic agents, of these aureomycin, streptomycin, terramycin, procaine-penicillin, and bacitracin have shown this growth promoting power. In each case, the optimal content in the diet for maximal growth has been found to be about 15μg. per g. food, or about ¼ lb. of antibiotic residue per ton of food.

Aureomycin and cobalamin have been reported to have a sparing action for each other, and a similar synergism has been reported for terramycin and cobalamin. The inclusion of antibiotics in the diet does not have a sparing action on carbohydrate, nor does it reduce the protein requirement, in fact, some workers have reported an increase in protein requirement from 20 per cent to 23 per cent for maximal growth. Birds reared on foods supplemented with antibiotics often suffer severe set-backs if for some reason this supplementation is discontinued.

A marked increase in liver vitamin A and serum carotenoid levels has been reported following the inclusion of procaine-penicillin in the diet, suggesting an increased capacity to absorb these from the alimentary canal.

Streptomycin, but not penicillin, had an inhibitory action on peristalsis in the isolated intestine. It appeared to act directly on the smooth muscle since it reduced the effects of histamine and acetylcholine.

In the laying hen, it was shown that while pullets raised from hatching on diets containing antibiotics grew faster, the mature weight was not affected. The age at sexual maturity and the rate of egg production were the same and the eggs were no larger after the addition of aureomycin to the diet. Nor were any beneficial effects noted in the efficiency of food utilization, mortality or broodiness.

When fertile eggs from hens receiving antibiotics in the diet were used for the cultivation of Rickettsia virus, the virus ceased to grow after the antibiotics had been fed for three weeks, although the eggs would still support the growth of the influenza virus. This finding indicates that antibiotics are absorbed by the fowl and that they can pass the membranes into the egg; other experimenters found that aureomycin disappeared from the blood stream in less than 24 hours after dosage.

The addition of antibiotics at the rate of 2 lb. per ton of food greatly reduced the incidence of coccidiosis. In one experiment chicks were injected with 150,000 coccidial cysts and then fed on diets with and without aureomycin. At the end of eight days the surviving birds were examined for symptoms of coccidiosis, with the results set out in Table 3.18.

TABLE 3.18

INCIDENCE OF COCCIDIOSIS 8 DAYS AFTER INJECTION WITH 150,000 CYSTS PER BIRD

	Incidence of coccidiosis in %				
	Fatal	*Severe*	*Medium*	*Mild*	*None*
Without aureomycin	37·5	37·5	25·0	0	0
With aureomycin	0	0	0	30·0	70·0

OTHER GROWTH PROMOTING SUBSTANCES

Grain distillers began using wetting agents to increase the efficiency of their processes, and, realizing that these wetting agents would remain in the distiller's solubles, conducted chick tests to determine their toxicity. They noted a consistently higher rate of growth in birds dosed with the wetting agent than in the controls. Nutrition workers have since found that many of these wetting, or surface active, agents are capable of stimulating the growth of chicks, as are ordinary soaps, 3-nitro-4-hydroxyphenyl arsonic acid—an organic arsenical compound,—and some of the sulphonamides.

MODE OF ACTION OF GROWTH PROMOTING SUBSTANCES

The mode of action of growth promoting substances is not clear. The organic arsenical compounds stimulated appetite and when the food intake was equalized with the control group the growth rates were the same; the surface active agents might be presumed to act by virtue of their wetting power increasing the absorption of food from the intestine, but as both are known to possess bactericidal activity this property cannot be ignored. The antibiotics were developed to combat bacteria, so this property does provide a common character for them all.

'Germ-free' chickens did not show a growth response to the antibiotics, whereas chicks kept normally at the same centre responded, supporting the view that the growth promoting substances produce their effects by the destruction or inhibition of micro-organisms in the alimentary tract which compete with the host for the available nutrients.

When chicks were reared in a new building, they grew as well without antibiotics as with them, and as well as a similar group of chicks fed antibiotics in an old building. This suggested the existence of a growth-depressing ' infection ' in the old building. The condition was found to be transmissible by contact or by feeding whole-gut contents, but its nature is still obscure.

The antibiotics have been reported to decrease the requirements of certain vitamins of the B group, notably those of the A.P.F. complex and the greatest response to their use has been obtained on all vegetable diets.

It may therefore be concluded that growth promoting agents act by (*a*) the suppression of some infectious condition whose main symptom is depressed rate of growth, (*b*) stimulation of appetite, and (*c*) in the case of the antibiotics, an indirect economy in some of the vitamins of the B group, notably those of the A.P.F. complex.

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CHAPTER 4

TRACE ELEMENTS

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PLANTS have the faculty of assimilating large amounts of certain elements out of proportion to their abundance in the soil, and animals have a similar but less pronounced ability to retain selectively certain elements from the plants they eat. Some of these in traces are essential to the animal but many others are found also in traces and whose presence has so far not been proved to be essential or innocuous. Animals require traces of iodine and cobalt and these they obtain from plants, but it has never been demonstrated that these elements are essential for the life of higher plants: on the other hand, the element boron is essential to plants but not to animals. The luxuriance of a plant is thus not necessarily a criterion of its mineral content, and the usual commercial fertilizers may or may not add to a deficient soil all that is needed.

A trace (sometimes referred to as ' minor ') element in the sense of this chapter is generally a metal—iodine and fluorine being exceptions —which is present in the organism in not more than 1 part in 20,000 normally and there subserves an essential function, most probably in some form of enzyme system, hormone or vitamin. Under the term of essential trace elements we group iron, cobalt, copper, manganese, zinc, iodine and fluorine, and now molybdenum must be added. In addition reference will be made to certain non-essential trace elements which are liable at times to reach the upper limits of safety in the food or water, namely arsenic, lead, mercury and selenium. For most trace elements there is a wide range between those quantities which by common consent are innocuous or essential to health and those which show signs of being injurious.

The distribution and the availability of the various chemical elements, including the trace elements, have been fundamentally controlled in broad outline by the chemical evolution of our planet during geological and pre-geological time. The distribution of trace constituents in soils depends to a great extent on the parent rock and its mode of formation. Trace constituents occur in soils in amounts from a fraction of one part per million upwards, and in different soils the amounts of any one may vary by as much as one thousandfold. The main factors governing the distribution of trace elements in minerals have been elucidated chiefly by GOLDSCHMIDT and his colleagues, but it would be out of place here to deal with this complex matter. Suffice to state that the distribution of many trace elements depends very much on their stage of oxidation. Iron, manganese, and cobalt are often immobilized as a result of the processes of oxidation ; selenium, arsenic, molybdenum may be mobilized by oxidation to readily soluble complex anions, in accordance with the rules of ionic potential. Many special peculiarities in the geochemical distribution of trace elements are due to special biochemical processes. Other trace elements owe their special mode of distribution to the circulation in the atmosphere and hydrosphere, *e.g.* the often air-borne iodine.

If the soil can be related directly to an igneous rock, the trace constituents can be foretold with reasonable accuracy, but where, as often happens in the north-east of Scotland, the soil is formed from glacial drift derived from sedimentary or metamorphic rocks, the problem is generally an individual one for each soil.

The total content of a soil gives little more than a guide to the possibility of the occurrence of a deficiency or excess of a given element. The greater proportion of any trace constituent present in a soil is generally bound up in the crystal lattices of the minerals and is quite unavailable until released by weathering.

If the crop is not removed the trace constituents which are taken up by the plant will tend to accumulate in a readily available soluble form in the surface organic litter at the expense of the lower layer of the soil. Zones of depletion or of accumulation of trace elements in the different horizons of the soil profile, resulting from normal processes of soil formation such as podzolization or lateritization, are also to be found but, as yet, it is not possible to generalize. On some soils, generally those rich in calcium carbonate, deficiencies in trace elements may occur in the vegetation, although abundant amounts are present in the soil.

Different species have different uptakes. Time of sampling and degree of maturity also affect the level found. Preferential grazing may leave those species which the animal does not eat and thus analysis of the pasture may give a wrong impression of the composition of the diet. A properly sampled pasture appears never to contain more than 150 p.p.m. of iron, generally 50 to 80 p.p.m. Higher levels usually indicate soil contamination. Sampling of soil and pasture is a highly specialized procedure and should only be undertaken after instruction by an expert.

For workers in the United Kingdom 'pine' is perhaps the outstanding example of a trace element deficiency, yet cobalt deficiency, leading to pining in sheep, is a deficiency which has no effect on the health of the pasture and cannot, therefore, like some other plant deficiencies, be diagnosed by visible leaf symptoms. It occurs in as widely scattered areas as the Orkneys, Hebrides, coast of Argyllshire, Northumberland, Dartmoor and North Wales. The first mention of 'pining' in the literature is probably that by JAMES HOGG, the Ettrick shepherd, in 1831, who even then realized that this was probably due to a nutritional deficiency. In 1928, GODDEN and GRIMMETT drew attention to the similarity between the condition of 'pining' as found in Scotland and 'bush sickness' described earlier by ASHTON in New Zealand and which was then believed to be due to a deficiency of iron. GREIG and his colleagues in 1933 described how the disease occurred on the island of Tiree on the west coast of Scotland, but only on those pastures of which the subsoil was sand and that it could be prevented and cured by the administration of iron compounds, but it was a puzzling feature of this result that the iron of the soil of the affected pastures was adequate. This same anomaly was noted by workers in Australia who later showed that the actual cause of the condition was a deficiency of cobalt and that the curative value of the iron lay in the traces of cobalt contained in its salts.

In 1932 LYLE STEWART described the lesion in the spinal cord of new born sheep and lambs suffering from 'swayback' or 'swingback' in Great Britain, the pathology of which has since been more extensively studied by INNES. Its resemblance to the enzootic ataxia of Australia and New Zealand was considerable and, as will be described later, is due to copper deficiency.

The development of our knowledge of these elements is a fascinating tale and in particular the disorders of stock in Australia caused by deficiency of cobalt and of both cobalt and copper. According to Sir CHARLES MARTIN who knows this portion of nutritional history intimately, the discovery that traces of cobalt of the order of 0·1 mg. daily for sheep and 0·5 mg. for cattle are required, was made simultaneously in 1933, though reported later, by two groups of investigators, FILMER and UNDERWOOD in Western Australia, and MARSTON, LINES and MCDONALD of South Australia. The reasons for the investigations which led to the discovery, were the same in both instances but the avenue of approach differed somewhat.

On the coasts of South Australia and Western Australia are to be found areas which have long been known by farmers to be unsuitable for raising sheep and cattle although they enjoy a rainfall of from 20 to 40 inches and produce an abundant herbage throughout a good proportion of the year. Animals could be fattened on these pastures, but if maintained upon them for more than three to four months they lost condition, became weak and, unless speedily removed to other pastures, wasted and died. Sheep which had not suffered too severely recovered rapidly after transference.

In South Australia the soil of these unsound patches of country consisted of windblown sand and shells, not yet consolidated. In Western Australia the areas where this disorder was noted consisted of a loamy gravel formed by weathering of old granitic rocks.

The symptoms of the disorder observed by **Filmer** in Western Australia were progressive emaciation and weakness and in the later stages, an anaemia of the normocytic type. Filmer suggested the name ' enzootic marasmus ' and concluded it to be the result of some nutritive deficiency.

In view of the general similarity between this enzootic marasmus and the bush sickness of New Zealand which Ashton had found amenable to treatment with large doses of iron, particularly in the form of limonite, pharmaceutical preparations of iron and limonite were given to sick animals. Nevertheless Filmer was not satisfied that it was iron which cured the animals, because of the massive doses required and the superiority of the crude mineral. He thought that it was more likely that the enzootic marasmus was due to a deficiency of some mineral present in the iron preparation. He was joined by Underwood in 1931 and together they tested the iron-free extract of limonite and found it effective, whereas the iron was not. They then searched for the potent element. After eliminating iron, manganese, and nickel, cobalt was tried as cobaltous chloride and found effective, the general condition of moderately severe cases improving immediately and the blood returning to normal in two months. Further experiments by these two showed that sick sheep could be cured and subsequently maintained in health on unsound farms for 14 months with a daily dose of 0·1 mg. cobalt by mouth; cattle required from 0·3 to 1·0 mg. daily to maintain health.

The investigation of the wasting disease affecting sheep grazing on the unconsolidated dune soils along the coast of South Australia which also led to the discovery that a small amount of cobalt was essential for sheep, was more difficult because as subsequently transpired, it was found that the sheep also suffered from copper deficiency. In addition to the emaciation and anaemia of enzootic marasmus described by Filmer, ataxia proceeding to complete incoordination of the movements of fore- and hind-quarters was frequently observed. These symptoms occurred more in lambs and young sheep and were shown by **Bull, Marston, Murnane** and **Lines** to be due to more or less extensive demyelination of some of the tracts of the spinal cord. The lesion was similar to that first adequately described by Lyle Stewart in 1932.

A survey of the incidence of these nervous symptoms indicated that two maladies of different causation were frequently superimposed on one another in the coastal area of South Australia. The ataxic disease was similar to, if not identical with that described by BENNETTS in 1932 and 1933 as occurring in a particular area in Western Australia where it was called ' gingin ' disease and was shown later by BENNETTS and CHAPMAN, 1937, to be due to a deficiency of copper. Bennetts called it enzootic ataxia. The acute wasting disease resembled bush sickness in New Zealand and enzootic marasmus as seen in Western Australia.

LINES in 1935 found that cobalt was effective but further trials were disappointing; some improvement occurred in the sheep but not complete cure. The explanation was not clear. The protocols show that copper was given shortly before the cobalt. Subsequently it was found that the gluten in the laboratory diet also contributed copper.

The final explanation came from the work of MARSTON and MCDONALD (1938), who tested out various combinations of zinc, iron, nickel, cobalt and manganese on sheep on the coast disease-producing pastures. The control group without any treatment and all those treated with various combinations which did not include both copper and cobalt succumbed within a year.

The so-called ' falling disease ' of cattle in Western Australia, characterized by cachexia, anaemia, suppression of oestrus in cows, and stunted abnormal appearance of calves is regarded as a simple copper deficiency by Bennetts and his co-workers. The picture is that of the terminal phase of an acute copper deficiency accompanied by transient anaemia.

These Australian discoveries in respect of cobalt were soon found to apply to the bush sickness and Morton Mains ' sheep ailment ', ' pine ' in the United Kingdom, ' nakuruitis ' of Kenya and the ' grand traverse ' disease of Michigan.

In 1938 in New Zealand, HOPKIRK and GRIMMETT and also MCNAUGHT (1938) worked out the minimum amount of cobalt which must be contained in a pasture to ensure the well-being of stock. This would appear to be 0·07 to 0·3 p.p.m. D.M. (0·07 to 0·3 μg./g. D.M.)* for sheep: and for cattle as little as 0·04 p.p.m. D.M. (0·04 μg./g. D.M.) was sufficient. Top dressing with half to one pound of a cobalt salt per acre rendered these pastures capable of maintaining stock in health for at least a year.

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*Sometimes in the literature concentrations of trace elements are expressed as parts per million on dry matter basis—p.p.m. D.M.—or micrograms per gramme of dry matter—μg./g.D.M. The latter expression is used in this chapter when reference is made to concentration in the tissues or indoor feeds, the former when applied to the soil or pasture or other outdoor fodder. The conversion is easy for the actual figures are not changed, the p.p.m. D.M. or μg./g. D.M. being added after the figure(s) according to the system used.

IRON

OCCURRENCE AND FUNCTION

Iron is the metal element occurring in animals about which most is known. The story of its function in the body has been built up with the progress of physiology and so no references are given. Iron is not usually regarded as a trace element because although it occurs in the body to the extent of 1 part in 25,000, in the blood it is present to the extent of 1 in 2,000 and there acts as an oxygen carrier rather than as a catalyst. It is interesting that with perhaps one exception of a very rare respiratory pigment haemerythrin in worms, iron always appears, wherever its physiological rôle is definitely established, as an iron-porphyrin-protein compound. In this complex compound the iron-porphyrin nucleus, known as haematin, forms the active prosthetic group of the molecule. Belonging to this iron-porphyrin-protein compounds are two categories of biologically important substances, the oxygen carriers and the oxidizing catalysts or enzymes.

An oxygen carrier is a compound capable of combining loosely with molecular oxygen, taking it up in places where it is available and giving it up where it is being used up and in consequence where its pressure is low. To this family of compounds belong the blood haemoglobins of vertebrates and muscle haemoglobin.

To the oxidizing catalysts belong the four components of the cytochrome system which play a fundamental part in intracellular respiration, and catalase also in an iron porphyrin. They are responsible for the transfer of hydrogen from the activated molecules of foodstuffs to the molecular oxygen. They thus catalyse the reaction of the combustion of hydrogen to water which liberates the large amount of energy necessary for the life of the cells.

At least two other enzymes are known to belong to the iron-porphyrin-protein compounds, one—peroxidase—catalyses the oxidation of substances by means of hydrogen peroxide; the other catalyses the decomposition of H_2O_2 into molecular oxygen and water.

These various activities exhibited by compounds with the same iron-porphyrin nucleus depend on the particular protein in combination.

Most of the iron in the body is present in the form of haemoglobin. Since the red cells and their haemoglobin are constantly being destroyed after some three months of existence and then replaced, iron undergoes a very active metabolism. Its synthesis into haemoglobin requires the presence of traces of copper and occurs throughout life as well as during the period of growth when the total blood volume is being built up.

The red cells originate as immature cells in the bone marrow and later pass to the main circulation where they develop into mature erythrocytes. During their development in the bone marrow and finally in the main circulation, haemoglobin is synthesized and gradually accumulates in these cells. The normal content of haemoglobin for most mammals lies within 10 to 15 g. per 100 ml. whole blood. In severe anaemia the value may fall to a half or even a third of this.

Iron is absorbed from the food in the intestinal tract direct into the blood stream, apparently in the form of ferrous iron. Ferric iron is readily reduced in acid solution. After absorption the amount of which may depend on the organism's requirement, the ferrous iron is absorbed and stored intracellularly in the form of ferritin, a combination of iron and a protein apoferritin. When the equilibrium between the cellular bound iron and the plasma iron which is in the form of an iron (ferric) complex is disturbed by a demand for iron this plasma bound iron yields up its iron for the synthesis of haemoglobin (iron now in the ferrous state), a process which requires the presence of traces of copper, and is made good from the intracellular protein bound iron. Surplus iron is deposited chiefly in the liver, the body being unable to excrete iron to any extent. The red cells not in demand are concentrated in the spleen which contracts when necessary to expel them. At the end of their life span the iron enters a pool for ready resynthesis into haemoglobin. Haemoglobin may be found concentrated also in the kidneys. Fibrosis occurs in organs heavily loaded with iron, *e.g.* in haemochromatosis. Oestrogens cause a rapid fall in plasma bound iron.

Iron is stored chiefly in the liver in combination with protein (presumably mainly ferritin). When there is a demand for iron the stored iron is used and replaced by increased absorption. The absorption of iron has been reduced experimentally by excess of calcium carbonate in the diet. As a result a hypochromic anaemia (too little haemoglobin in the cells) may arise with lipaemia and increased fat deposition and with adverse effects on breeding performance. This effect does not arise with calcium phosphates.

When the red blood cells become effete their haemoglobin is broken down, but the iron is conserved in the body for the resynthesis of haemoglobin in maturing red cells. Negligible quantities of iron are excreted in urine or faeces, in the case of the latter largely due to the presence of desquamated epithelial cells, that found in the faeces representing unabsorbed iron. Thus there is a considerable degree of economy exercised in the use of iron.

It is generally held that the blood pigments have no dietetic value as suppliers of iron. Besides porphyrins there are apparently other iron-containing organic compounds in which iron is not available, such compounds, for instance, as double phosphates of ferric iron with organic complexes in which the iron is not easily dissociated in acid solution. The nature and amount of the phosphates present in food and the calcium-phosphorus ratio may have a considerable influence on the availability. Pyrophosphates and metaphosphates in solution are well known to have the property of de-ionizing ferric iron. Presumably this may also occur in the alimentary tract. Of the organic compounds of phosphoric acid which can combine with and deionize iron, phytic acid (inositol hexaphosphoric acid) is the most important. In pigs at least it seems fairly certain that a phytase occurs in the gut which splits off the phosphoric acid.

EXPERIMENTAL ANAEMIA DUE TO IRON AND/OR COPPER DEFICIENCY

The morphological and biochemical similarities in pigs due to iron deficiency, copper being adequate, and that due to copper deficiency, iron being adequate, are striking, and recent work from the United States (LAHE *et al*, 1952) has indicated the following features in common in experimentally induced deficiencies: microcytic hypochromic anaemia, normoblastic hyperplasia of bone marrow, low blood iron, and an increase in the iron-binding capacity of the blood. The differences were few: in copper deficiency the white cells were moderately reduced; in the iron deficiency the counts were normal. Thus it seems possible that copper is in some way essential for the absorption, transportation, storage and utilization of iron by the bone marrow and that in the absence of copper, anaemia develops as a result of failure to metabolize iron properly. It is further suggested that in the absence of both copper and iron from the diet, anaemia develops more rapidly than when either element alone is absent.

In pigs made anaemic by feeding a milk diet low in copper (cow's milk treated with sodium sulphide) there is impaired ability to absorb iron from the alimentary tract or to utilize parenterally administered iron for haemoglobin synthesis, and to effect the complete mobilization of iron from the tissues.

Iron is abundant in the soil but plants only require a small amount and this is made available by the action of humus and thus the more acid the soil the more liable is it to contain soluble salts of iron.

NUTRITIONAL ANAEMIA DUE TO IRON DEFICIENCY

Nutritional anaemia due to lack of iron is particularly likely to develop in certain species during the suckling period, since milk is very low in iron; but it may occur at any time of life when the available supply of the mineral becomes deficient relative to the needs for haemoglobin formation.

In a comparison made between the mineral constituents of milk and of the newborn it was found that while the other constituents were in similar concentrations the percentage of iron in the milk ash was only one-sixth of the figure for the iron in the ash of the newborn. It was also found that in the newborn there was a much larger percentage of iron present at birth than later in life (guinea-pig excepted). The apparent explanation is that the iron requirements for the suckling animal are largely looked after by means of a store built up in the liver *in utero,* so that after birth it can be drawn upon for haemoglobin formation and the necessary enzyme systems already described.

However, the natural provision of iron for the suckling animal does not seem to be optimal for some species. If birth is premature then there is a smaller store because most of the storage takes place in late gestation. Further, if the breeding policy has been to secure larger and still larger litters as, for example, in pigs, the individual's supply tends to be smaller. Even if the store is normal, a long nursing period without access to soil or supplementary iron-rich food may not permit adequate supply, particularly is this the case with unthrifty animals which are usually longer in taking to creep feeding of any considerable extent. The evidence indicates that most of the iron obtained by the piglet during suckling is obtained from its surroundings. In rabbits even though the liver contains a largish store little is withdrawn during suckling. If piglets are kept indoors on concrete floors their haemoglobin level is lower than that of those weaned out of doors or allowed out for a few hours with access to soil. The lower liveweight and haemoglobin are improved by giving iron and it is important that some form of this should be administered within three days of birth. A further dose should be administered at about 10 days of age and as a further precaution a third dose could be given at 17 days.

The two most satisfactory forms of iron are ferrous sulphate and reduced iron. Although copper is necessary for haemoglobin formation there is no need to dose young pigs with a copper salt even though the form of iron used is copper-free. The dose of ferrous sulphate is about 0·25 g.; that of reduced iron from 0·1 g. to 0·3 g. One worker gave 1·0 g. of a mixture of 2·1 parts reduced iron and 7·9 parts glucose. The use of a diluent has practical advantages. As an alternative to dosing, piglets may have access to a mixture of about one ounce of dry ferrous sulphate with 150 lb. soil but this method does not give as sure results as dosing.

The feeding of iron to the sow during pregnancy or lactation fails to influence the level in the milk. Iron deficiency in farm animals is thus essentially limited to iron deficiency in pigs when these have not access to soil. Calves begin to take supplementary food at any early stage which is generally of such a nature that it supplies iron.

Iron-deficiency anaemia can occur beyond the suckling stage, indeed at any time of life when the supply is inadequate to meet the demands for haemoglobin formation. Gestation naturally makes special demands, so also does egg production. However, the ubiquity of iron in the commonly fed rations, leaves and seeds in particular, especially the germ and outer coatings of the latter, is such that uncomplicated iron deficiency disorders do not usually occur even though the availability may be low.

In Florida is to be found a condition in cattle which seems to be largely due to a deficiency of iron and copper, for the animals receiving a ration consisting mainly of a particular grass forage crop become anaemic and respond to iron and copper treatment.

COBALT

The history of the discovery that the cause of much debilitating illness amongst ruminants, sheep in particular, was due to a lack of sufficiency of cobalt in the plants eaten has already been set forth in the introduction. It demonstrates the period of time which may exist between the early observation of an illness amongst stock and the discovery of its root cause.

Very shortly after the demonstration in both Western Australia and South Australia that small supplements of soluble cobalt salts, administered by mouth, could not only effectively prevent ' pining ' or what was termed ' enzootic marasmus ' in Western Australia, but would also restore normal health to animals that had developed the condition and that dramatic responses also occurred in Coast disease even though this was a combined cobalt and copper deficiency, bush sickness of New Zealand; salt sickness of Florida; pine in Scotland and England; nakuruitis of Kenya in East Africa, were all reported to respond to cobalt. At a rather later date similar evidence was obtained from many other parts, namely, from the United States of America, Canada, Ireland, Norway, Denmark, Sweden and Estonia. There is probably no doubt that between a normal intake and an intake so low as to lead to frank pining, there is an area where a relative shortage affects the health and productivity of grazing ruminants, particularly young animals. Such subclinical forms may become manifest in a subacute or acute form by change of season.

The severity of the syndrome and the lack of cobalt in the available fodder, in so far as this is judged from chemical analyses of pasture samples, principally by spectrographic means, run in parallel: the deficiency in the plant is the result of a deficiency in available cobalt in the soil. When seasonal outbreaks occur they are frequently, though not always, the consequence of a rapid growth of grass on an incipiently deficient terrain. Grasses in general appear to contain less cobalt than other fodder plants where the soils are short in this element.

SYMPTOMS OF COBALT DEFICIENCY

The symptoms of cobalt deficiency in the sheep consist of a progressively wasting disease coupled in many areas, but not apparently in Scotland, with a profound anaemia (Stewart and Holman, 1944).

The absence of any marked degree of anaemia in this country indicates that the anaemia, if it occurs, is rather an expression of malnutrition than the essential lesion. There is failure of appetite and consequent emaciation and lethargy. The skin and exposed mucosal surfaces are pale, the former may be fragile in extreme cases. In severe cases the blood volume and plasma protein concentration are materially reduced and Australian workers have reported that the oxygen-carrying capacity falls to 30 per cent of normal or lower—the degree varying with the severity. They suggest that the blood picture in the early stages of the disease is that of an aplastic condition of the bone marrow and that as the condition worsens there is a profound macrocytic anaemia with marked poikilocytosis, and polychromasia supervenes. In the acute form, appetite fails to such an extent that death supervenes through inanition. There are no obvious nervous sequelae.

These findings are the extreme consequences in sheep confined to fodder that is markedly short of cobalt. With less severe restriction in intake the growth rate of the lamb is seriously impaired and the adult loses weight but does not exhibit any obviously specific clinical signs. Indeed the ewes can carry lambs to full term, even when in an advanced stage of the acute syndrome. However, the lamb which is born either succumbs within a few days of birth or is sickly and grows very slowly depending on the degree of deficiency.

The syndrome in cattle is similar but not so spectacular. Young, growing animals are particularly prone—they become unthrifty and anaemic. The calves born of cobalt-deficient cows are weak and scarcely survive more than a week. The degree of cobalt deficiency usually prevalent in pastures on deficient terrain leads to a subacute state of deficiency which leads to unthriftiness in the cows, lack of milk, and the calves develop a general cachexia.

PREVENTION AND CURE

The therapeutic test is the only sure diagnosis. Provision of cobalt by mouth at apparently any stage will arrest the condition and once a normal cobalt intake is achieved the animals rapidly recover appetite and their normal health.

Work, particularly in Australia, indicates that a total ingestion of 0·07 to 0·08 mg. of cobalt daily is close to the quantity that will completely fulfil the requirements of sheep, and that a fodder containing 0·08 to 0·10 p.p.m. on a dry matter basis is probably about the lower limit of security in respect to cobalt. The bovine requirement is not known with such definition but it is not unlikely that it will be of the same general order as that for sheep. Certainly 1 mg. per day is sufficient. In some areas the deficiency is rectified by fertilizing at the rate of ½ to 1 lb. of cobalt sulphate per acre. For United Kingdom conditions it has been found that for arable land under the normal course of rotation, the application of cobalt sulphate at the rate of 2 lb. per acre to the young grass raises the cobalt status for 3 years at least, provided the *p*H of the soil is not above 6·5. The mode of application is as a top dressing in admixture with superphosphate. On hill land the whole question of amount, frequency and mode of application is still under investigation.

It is necessary to stress that when ruminants are dosed with cobalt this must be ingested. It is largely valueless when injected into the bloodstream even though by this means the level is maintained at a very much higher point than normal. Cobalt must be ingested frequently: it has been found effective when given thrice weekly. Its zone of action appears to be above the duodenum. After absorption or injection, part is excreted in the bile and appears in the faeces apparently not having been absorbed in its passage. Some of the injected cobalt which appears in the bile may pass back to the rumen but only in minute traces.

EFFECTS OF COBALT TREATMENT

In the cobalt-deficient ruminant there is a change in the flora of the rumen and the numbers of micro-organisms are reduced if the cobalt intake falls below requirement. Digestion of crude fibre is said not to be impaired. If this is true, the effect of cobalt deficiency may be due to a depression of bacterial synthesis of accessory food factors.

Unlike human pernicious anaemia, the anaemia of cobalt deficiency —when it occurs—is not responsive to parenteral injection of liver extract in quantities similar to those used in pernicious anaemia.

The finding that vitamin B_{12} is a cobalt-containing complex, curative in human pernicious anaemia, and produced in rumen contents and that the rate of its synthesis both there and in the lower levels of the alimentary tract is seriously diminished when the concentration of cobalt in the ingesta is low, suggested that the syndrome in ruminants might be due to a shortage of vitamin B_{12}. Early attempts to cure cobalt deficiency using it *per os* or parenterally had been just as unsuccessful as happened with liver extract, but thus far the treatment tried had been on the human level of dosage. Then came information that injection of the equivalent of 15 U.S.P. units of a purified liver extract per diem prevented the onset of the syndrome of cobalt deficiency in lambs confined to a deficient ration and now we have information that parenteral injection of much larger quantities of pure vitamin B_{12} than those previously employed gives a positive response in cobalt-deficient lambs (Becker and Smith, 1951). Workers in Australia and New Zealand have confirmed this finding. The blood and general condition in these cases responded to this high dosage.

It is generally considered that cobalt functions in all species in connection with its direct haemopoietic action and that in ruminants there is an additional requirement concerned with the function of cobalt in rumen contents which is probably related to microbial action and the production of B-vitamins. In support of this it has now been found that after oral administration of radioactive cobalt considerable biosynthesis of vitamin B_{12} occurs in the alimentary tract, probably mainly in the rumen. After intravenous administration there is only slight, if any, biosynthesis in the tract, but considerable formation of vitamin B_{12} in the tissues with the suggestion that the adrenals and spleen are mainly responsible. Overall, more than 10 times as much radioactive cobalt is converted to B_{12} after ingestion than after intravenous administration. The concentrations of vitamin B_{12} like bound cobalt in the tissues after intravenous injection are slightly higher than after ingestion of equal amounts of cobalt. The evidence indicates that vitamin B_{12}-like material being synthesized by the tissues from inorganic cobalt is physiologically ineffective in relieving cobalt-deficiency in sheep. It has been generally concluded from this that the syndrome of cobalt deficiency in the sheep is the result of a profound vitamin B_{12} deficiency.

A series of experiments with Merino ewes confined in metabolism cages and fed on cobalt-deficient rations has indicated that activity of the micro-organisms responsible for the fermentation of carbohydrate in the rumen remains unimpaired when the cobalt concentration of the fodder is reduced to a level which induces the profound deficiency syndrome in the animal, as critical balance experiments have proved that the digestibility of the rations remains unaltered in these circumstances. The failure of appetite which is the first symptom to appear and which is progressive, is thus the result of a metabolic defect and not due to a reduced capacity of the animal to digest and absorb foodstuffs. Neither cobalt (*per os*) nor vitamin B_{12} (parenteral) effected any change in the overall digestibility of the fodder although a considerable alteration in the nature of the microbial population of the intestinal tract of the animal which received a supplement of cobalt is implied by the increase in the vitamin B_{12} activity of its faeces. MARSTON and SMITH (1952) feel confident in stating that the syndrome of cobalt deficiency in the ruminant is the result of a metabolic defect arising from a profound deficiency of vitamin B_{12}. There is as yet no evidence that cobalt performs any physiological function in the tissues of animals other than as a constituent of vitamin B_{12}.

Further observations from Australia indicate that after treatment of cobalt-deficient sheep with cobalt (1 mg. per day *per os*) there was an increased concentration of vitamin B_{12} in the faeces. Injection of vitamin B_{12} (50 μg. per day) into the animals had no appreciable effect on the vitamin B_{12}-like activity of a given weight of faeces. It would seem from their work that there are at least ' B_{12}-like factors ' in sheep faeces and that their absolute and relative concentrations depend upon the level of available cobalt in the gut.

It is broadly true to state that vitamin B_{12} is essential for animals and that the higher plants are devoid of it. Vitamin B_{12} is unique among accessory food factors in that it originates only in micro-organisms. It is out of place here to discuss vitamin B_{12} and the animal protein factor: the reader is referred to pages 84 and 136.

COBALT REQUIREMENTS OF NON-RUMINANTS

The fact that horses, rabbits and marsupials do well when restricted to seriously cobalt-deficient fodder, suggests that ruminants are unique in their greater demands for cobalt. So far, all attempts to produce cobalt deficiency in small laboratory animals have failed but in these experiments there has been an adequate supply of vitamin B_{12} and the habit of coprophagy by rabbits would tend to reduce their exogenous requirements.

ABSORPTION AND EXCRETION OF COBALT

About one third to one half of the cobalt ingested by the sheep is absorbed and that not retained is excreted mainly in the urine. The cobalt excreted in the faeces represents for the most part, the fraction unabsorbed from the intestine ; a small fraction comes from the bile.

Cobalt is not excreted in the saliva or in pancreatic secretions and so far there has been but little detectable radioactivity in the rumen contents after injecting radioactive cobalt into the bloodstream of cattle; though there is evidence that cobalt has been found in the rumen of sheep fed a cobalt-deficient diet with cobalt introduced by duodenal fistula.

Evidence from human subjects and laboratory animals suggests that vitamin B_{12} even when free, is absorbed from the upper levels of the alimentary tract, and then only if combined with a factor present in the gastric secretions. In the light of the apparent large requirement of B_{12} by the ruminant the supply is secure if enough cobalt is fed so that sufficient of the vitamin can be synthesized in the rumen prior to the passage of the ingesta through the tract. Non-ruminant herbivora must derive their requirements from sources other than what is considered to be their normal fodder if they cannot absorb vitamin B_{12} from the lower levels of the gut. Coprophagy universal among rabbits, and possibly in many more herbivora, provides a means of ingesting and absorbing vitamin B_{12} synthesized by micro-organisms in the gut at a level which is not compatible with efficient absorption. The observation that the top layers of soil contain vitamin B_{12} is of great interest as most grazing and rooting animals like the pig, perchance consume considerable quantities of soil.

LESTER SMITH (1951) in reviewing the subject has shown that in the rat only about 40 per cent of vitamin B_{12} remains intact during its passage through the alimentary tract.

It has been found that the administration of extra cobalt to lactating ewes produced a highly significant increase in the vitamin B_{12} content of their milk compared with ewes receiving no cobalt.

EFFECTS OF EXCESS COBALT

Since the original observations by WALTNER and WALTNER in 1929 that excess cobalt, whether given orally or parenterally, induces a polycythaemia in rats, this increase in red cells has been noted in all species of animals studied. First there is a hyperplasia of the bone marrow and a marked reticulocytosis. Cysteine, in amounts sufficient to form a stable association complex with cobalt when simultaneously administered, lessens considerably the erythropoietic effect. This suggests that the effects of the excess of cobalt are due primarily to fixation of thiol (-SH) groups within the tissues. Histidine, which is known to induce a reticulocytosis in cases of secondary anaemia of pregnancy in humans, is also known to chelate with cobalt, and has a somewhat comparable but less complete protective action against cobalt-induced polycythaemia in the rat; it has also been reported to prevent *in vitro* the respiratory depression brought about in micro-organisms and in animal tissues by excessive dosage with cobalt.

The very wide gap between the quantity of cobalt necessary to fulfil the nutritional requirements of ruminants and the toxic limits for sheep and for cattle are such as to render the chance of overdosage in husbandry practice unlikely and should not admit any retardation of administering cobalt on the ground where needed, even by aircraft.

VITAMIN B_{12}

In 1948 the biological function of cobalt was greatly advanced by the simultaneous discovery in the United States (RICKES and his colleagues) and the United Kingdom (Lester Smith) of vitamin B_{12}, a crystalline co-ordination complex of cobalt found in liver and also as the result of microbial activity. There are other very closely related cobalt complexes which differ only in the nature of the radicle which is attached rather loosely to the cobalt atom. The cobalt in the vitamin B_{12} group of complexes is in the trivalent state and is firmly bound. In all that has been mentioned here the term vitamin B_{12} implies physiological activity of vitamin B_{12} and of the other members of the group of cobalt-containing accessory food factors. It seems reasonably certain that these related complexes may all be converted *in vivo* to the physiologically active complex without appreciable loss of potency.

Vitamin B_{12}-deficient animals apparently suffer no nervous sequelae similar to the subacute combined degeneration associated with

Addisonian pernicious anaemia in man. Therapy in man with vitamin B_{12} leads to complete remission of all symptoms.

Although the part played by vitamin B_{12} in the metabolism of methyl-groups so far as transmethylation is concerned is still being investigated, the published evidence at present available suggests that even when the supply of vitamin B_{12} is optimal, a source of labile methyl-groups, such as choline or methionine, is an essential dietary constituent for very young animals, if they are to develop normally after weaning. Later on preformed methyl-groups can more readily be dispensed with, provided an adequate supply of vitamin B_{12} is available, for the animals can then probably synthesize methyl-groups at a pace sufficient to fulfil the physiological requirements of maintenance.

COPPER

Copper is probably an indispensable constituent of all living cells and it assumes a concentration pattern which indicates a correlation between copper and cellular activity. The copper-containing oxidases serve specialized physiological processes but are not found in all cells. Butryl-coenzyme A-dehydrogenase is a cupro-flavoprotein.

Copper replaces iron in the blood pigments of crustacea. In higher animals it plays a part in the utilization of iron for haemoglobin formation, not so much by increasing the absorption of iron as by its incorporation in haemoglobin.

SYMPTOMS OF COPPER DEFICIENCY IN ANIMALS

The work of ELVEHJEM from 1924 onwards at Wisconsin (reviewed 1935) on milk anaemia in rats showed that cow's milk is particularly short of both copper and iron but if supplemented with these, provides a ' complete ' food. By treating milk with H_2S a virtually copper-free milk can be obtained for work on animals. When animals are confined to this diet a well-defined deficiency state arises and if continued, this proceeds to a fatal termination.

During the course of the deterioration in copper status, specific symptoms which reflect individual metabolic defects appear in turn: thus the growth of the young animal decreases and the hair becomes harsh and, if pigmented, loses its colour before anaemia and other signs of an impaired iron metabolism become apparent, the animal then worsens progressively to a fatal termination. As the syndrome progresses the concentrations of copper in the blood and in the liver fall steadily to very low levels. Provision of sufficient copper leads to rapid recovery to normality. These symptoms are shown by all animals tested when the effective copper status of the tissues falls below the level that can provide for physiological requirements.

COPPER DEFICIENCY IN RUMINANTS

The debilitating disorders exhibiting specific signs and symptoms now known to be attributable in livestock to a deficiency of copper have already been briefly mentioned. Their aetiology remained obscure until recently.

The first satisfactory evidence of a state of copper deficiency in grazing ruminants was the demonstration by SJOLLEMA in Holland in 1933 that dosing with copper resolved the cachectic condition common among cattle grazing on parts of the reclamation areas of the north-eastern provinces of Holland. Disorders which yield to treatment with copper have been recognized in cattle in other parts of Holland, in certain areas of Florida, Australia, England, Scotland, Ireland, Norway, Sweden, Germany, New Zealand, and almost certainly in other parts. A very rapid alteration of the red cells to a thorn apple shape has been reported from Holland when cattle have been transferred to copper-deficient pasture, and haemoglobinuria has been found.

As described in the introduction, a survey of the earlier literature indicates that the cause of the obscurity was due to the fact that in some areas there was also a complicating cobalt deficiency as in the Coast disease of Southern Australia, and in addition the copper status of grazing ruminants has sometimes been found to be adversely influenced ingestion of excess of other elements due to their concentration at times in the pasture.

Marston considers that the first claim that the disorder called ‘ Salt Sickness ’ which affects cattle in Florida, was due to copper deficiency, and the controversy which surrounded the claim that ‘ Lechsucht ’ and other similar disorders prevalent in north-western Europe were the result of copper deficiency, may now be resolved in the light of the probability that the observed syndromes were at times complicated by factors other than copper deficiency.

Although copper deficiency may manifest itself in adult sheep by such symptoms as emaciation, persistent diarrhoea, low liver copper values and in some situations, by poor wool quality and anaemia, but not generally in Britain, it is among young lambs born of such ewes that the most characteristic features of this deficiency may be found. When pregnant ewes have been grazing such areas for some considerable time prior to lambing (6–8 months) it is commonly found that the lambs develop signs of spastic paralysis and muscular incoordination—particularly of the hind limbs—hence in Australia and New Zealand the disease is known as ‘ enzootic ataxia ’ and in Britain as ‘ swayback ’.

SYMPTOMS OF DEFICIENCY IN RUMINANTS

Insufficient copper in the fodder of cattle leads to characteristic changes in the coat of the animals, for a specific change occurs which causes the hair to lose its capacity to produce pigment and become harsh, disordered and lacking in lustre. There is a very considerable loss of appetite. The wasting and the anaemia which supervene are not specific. The bones have been reported to become light and fragile and reproductive capacity is reduced and lactation seriously affected.

Young cattle are unthrifty and occasionally develop an ataxic condition of the hind limbs but this does not seem to have been investigated in a comparable fashion to the studies on the histopathology of the condition in sheep. In adult cattle the copper deficiency is stated frequently to terminate in heart failure due to atrophic changes in the myocardium.

The normal concentration of copper in the blood is about 1 μg./ml. and according to the degree of deficiency levels down to 0·2 μg./ml. or even less are found and the reserve of copper which is normally concentrated in the liver may fall from a normal of around 200 μg./g. dry matter to as low as 2 μg./g. Where anaemia results it sometimes progresses until the oxygen-carrying capacity is very low, at times down to less than a third of normal. There is also persistent and profuse scouring and the more persistent this is, the more rapid the wasting and the skeletal change.

The picture of uncomplicated copper deficiency is found in sheep grazing the southern Australian littoral and its nearby hinterland. There the soils are derived from aeolian sands of marine origin carried inland in recent geological times from an exposed continental shelf. Copper is so short that many plants are unable to complete their life-cycle unless extra copper is provided. The plants there contain rarely more than 4 μg. Cu/g. dry matter and frequently much less.

Mature sheep grazed there are unable to maintain their copper reserves and the copper level in the liver falls from 200 μg./g. D.M. to less than 5 μg. and in the blood the level falls from 1·0 μg. Cu/ml. to less than 0·1 μg. The first lesions to appear are those associated with defective keratinization and these occur when the blood level is down to about 0·3 μg. Cu/ml. This will be discussed later. As the condition worsens there is progression in the state of the hypochromic anaemia which is a reflection of disordered iron metabolism, and haemosiderin—an iron-containing product of haemoglobin break-down—is found deposited in the tissues.

If the concentration of copper in the liver of the pregnant ewe falls below 20 μg./g. D.M. nervous sequelae develop in the lamb and if the level falls lower than 10 μg. this is coupled with an extensive demyelination in the central nervous system of the lamb. Similar symptoms are known to occur in sheep grazed in areas where the copper concentration of the fodder is relatively high, with higher than normal concentration of copper in the blood. Complete prophylaxis of this condition can also be effected by a supply of copper.

The effects that supervene on an excessive ingestion of molybdenum and which have been suspected to be involved in the induced copper-deficiency syndrome will be discussed later.

COPPER AND DEMYELINATING DISEASE IN SHEEP

Mention has been made of the nervous affection of lambs born of ewes whose copper reserves are very low. The conditions because of the incoordination of the limbs, and sometimes blindness, has been called ' swayback ', ' swingle back ', etc. in the United Kingdom. Similar symptoms have been reported to prevail in young lambs from ewes grazing on certain areas of Peru, Sweden, South Africa, India, and particularly in New Zealand and in Australia where the name ' enzootic ataxia ' has been applied. The characteristic lesion is a diffuse, symmetrical demyelination of the central nervous system, the extent of the degenerative change varying from small foci in the cerebral white matter of the brain to a gross demyelination of both cerebral hemispheres and the formation of cavities. Secondary demyelination invariably follows and, according to the degree of degeneration, symptoms from a slight spasticity to a complete paralysis of the newborn lamb may appear.

The disease frequently originates *in utero* but it occasionally appears in young sheep a year or more after birth and it has also been noted in adult sheep reared in a copper-adequate area and later for experimental purposes transferred to seriously deficient fodder. It is rare, however, to see adult sheep with marked symptoms as such animals would usually succumb before severe symptoms appeared. The fact that the administration of copper to the ewe, if given in time, will protect the lamb, confirms the conclusion that it is due to a copper deficiency.

In the United Kingdom blood copper values are frequently low but diagnosis by blood analysis is of little value as ewes with a low blood copper level frequently give birth to normal lambs. Chemical analyses of herbage from affected areas in Britain indicate an apparent adequacy of copper.

Within the last year or two ALLCROFT and GREEN (1951) have reported a number of outbreaks of hypocuprosis in cattle, again many of them occurring on pastures of normal copper content. A ' copper pine ' of calves has been found in the county of Caithness and is characterized by greying of the hair in dark coloured breeds, coupled with a progressive emaciation which may terminate in death. ' Copper pine ' may be cured by intravenous injection or oral administration of small quantities of copper. Because of the apparently normal copper content of herbage in these areas where copper deficiency of livestock (frequently there is reduced concentration of copper in the blood) is found, it would seem that some 'conditioning factor' must render dietary copper relatively non-available to the animal. It has been suggested that high molybdenum or lead intake might be the conducive factor but recent work has indicated that neither of these elements is involved. Another suggestion is that some organic factor is causing interference with the normal process of copper absorption and utilization, either by direct 'binding' of herbage copper by organic complex formation or by a more direct effect upon the metabolism of the animal. Mills (1951) has shown that the copper of herbage exists in the form of organic complexes and that a number of the water-soluble copper complexes found in 'normal' herbage are absent in 'affected' pasture. The significance of these findings cannot be assessed until the mechanism whereby copper is absorbed from the digestive tract is more fully understood. As a small supplement of copper sulphate provides complete prophylaxis in this particular condition it suggests that the copper in the blood and tissues of the ewe is in a state which cannot easily traverse the placenta, and that the copper which does find its way into the foetus is unavailable for the nutrition of the nervous system. If this is so, this particular disorder might be considered to be the result of an induced copper deficiency. In Britain, ewes in swayback areas may themselves appear healthy and there is usually no anaemia and the 'stringy wool' common in Australia is not shown.

Copper pining of calves and swayback in sheep are not always found coexisting in a given area. This may indicate either that two causative factors are operative or may merely be a reflection of differences in nutritional management of calf and sheep flocks.

COPPER IN THE TISSUES AND SECRETIONS

The liver provides the main reserve supply which is drawn on when the intake of copper is insufficient to make good that which is lost in the secretions and excreta. The young bovine is born with quite a considerable store in the liver, the amount being from five to ten times more in the foetus than in the adult liver. In the case of the sheep, the concentration of copper in the liver of ewes varies from < 5 μg. in seriously deficient ewes to 600 μg. Cu/g. D.M. in the liver of ewes that have received a moderate excess of copper over a period of two years. It has been found that the total content of copper in the liver of the foetus becomes increasingly variable towards full-term and in the newborn lamb this variability often extends to twins.

Copper is not readily secreted by the mammary glands ; its concentration in the milk is always very considerably lower than that of the blood plasma and it is not readily influenced by changes in the latter. The concentration of copper in the colostrum is much higher than that of the milk and in the ewe at least reflects the concentration of copper in the blood.

The normal mean copper content of the blood of farm stock is close on 1 μg./ml. from which it may deviate quite considerably for a short period without untoward effects. It occurs in both the plasma and the cells, the latter containing about two-thirds of the former's content. A level persistently below 0·6 μg. Cu/ml. normally indicates a seriously depleted copper status and a persistent level above 1·3 μg. usually indicates treatment with copper in excess of requirement. When there is an excess of molybdenum in the diet a persistently high blood-copper concentration may be associated with a seriously reduced copper status.

ABSORPTION AND EXCRETION

Copper behaves differently from iron which, once absorbed, is conserved and only lost in minute amounts except through bleeding; copper is lost continuously, though slowly, in the excreta and must be replenished from dietary sources. A very small portion of the copper in the foodstuffs is absorbed by the animal; the major part is voided in the faeces. The main location of its absorption is the upper jejunum. Bile always contains copper and is probably the main route of its excretion.

EFFECTS OF CHRONIC EXCESS OF COPPER

Chronic ingestion of copper in moderate excess of the quantity necessary to establish nutritional equilibrium leads to its passive accumulation in the tissues. In such circumstances and depending on the nature of the fodder, the concentration of copper in the liver of the sheep increases more or less rapidly to very high levels—ten to twenty times that of the normal range—without any untoward physiological effects until for reasons not properly understood, there is a large influx into the bloodstream when excessive haemolysis may occur. Then there is haemoglobinuria and kidney failure—the kidneys being engorged and found gunmetal-coloured at *post mortem.*

British breeds appear to be more prone to succumb than Merinos to such catastrophic occurrences. Regeneration of red cells occurs between such crises though if the situation continues, death may ensue, generally due to liver atrophy. Such occurrences may result among sheep grazing in orchards and vineyards sprayed with copper-containing fungicides. It has also happened in Texas and elsewhere when sheep were allowed unrestrained access to salt licks to which tobacco dust and copper sulphate had been added in an attempt to control parasitic helminths. Apart from such happenings, sheep grazing certain areas untreated with copper accumulate abnormally high concentrations of copper in their livers, for example, sheep grazing areas in which subterranean clover is a dominant species accumulate abnormally high quantities of copper in their livers; although the available fodder there does not contain an excess.

BULL, ALBISTON and EDGAR (1944) have drawn attention to the syndrome of chronic copper poisoning which supervenes in sheep that previously have consumed the herbaceous plant *Heliotropium europaeum*; and there is suggestive evidence that a hepatoxic substance, possibly lasiocarpine, which this plant contains, induces slow, progressive pathological changes in liver cells which favour accumulation of copper.

Haemolytic jaundice in cattle has been reported when the animals have been dosed with large amounts of copper, but in general cattle exhibit a lesser tendency to accumulate copper.

COPPER IN IRON METABOLISM

When HART and his associates (1925) had shown how the anaemia which develops in animals confined to rations comprised solely of milk, responds to iron therapy only if copper is provided, subsequent work confirmed that copper functions in the utilization of iron. The microcytic hypochromic anaemia which is prominent in copper deficiency is practically identical to that which supervenes in iron deficiency. Copper does not apparently influence the absorption of iron except through a generalized action which assists in its metabolism. In copper deficiency it accumulates in the tissues and haemosiderosis results, particularly in the liver.

COPPER AND PIGMENTATION OF HAIR

Depigmentation of the hair occurs in copper deficiency but the physiological mechanisms are not yet satisfactorily understood; nutritional studies suggest that these may be very complex, for depigmentation occurs in other deficiencies. The evidence that pantothenic acid may be directly involved in copper metabolism is suggestive and it might be involved in the linkage of copper to the protein part of the polyphenoloxidases which produce melanin from L-tyrosine.

In addition to effects on pigmentation copper deficiency induces changes in the fleece, particularly of the Merino sheep. As the animal's reserves are depleted, the close, even crimp of the normal wool becomes less and less distinct in the newly grown staple, until the fibres emerge from the follicles as a wavy, characterless, hairlike growth, entirely devoid of crimp. On dosing the deficient animal with copper, the ability of the follicles to impart crimp returns with dramatic suddenness and the subsequent growth resumes its normal character. The chemical lesion appears to be a lowered efficiency of the chemical mechanisms in the follicles which convert the free thiol groups of the prekeratin molecules to the disulphide groups that provide the cross linkages in keratin proper. Application of a histochemical reaction of Girond and Bulliard by Marston by which free thiol groups may be rendered visible, has revealed that the transition zone in which reduced (-SH) prekeratin exists at the base of the normal wool fibre prior to its conversion to (-S-S-) keratin is increased tenfold or more in the fibres of the copper-deficient sheep. It is reported that there is no gross change in their amino-acid constitution. The observations fit a theory that copper ions or a copper-containing enzyme catalyse the oxidation of thiol to disulphide groups.

Besides being straight, the wool grown by black Merino sheep is unpigmented when the animal's copper status is seriously reduced. Treatment with copper sulphate, either by dosing or by application of very dilute solutions to the skin immediately reinstates to the follicles both the capacity to impart crimp and the ability to produce pigment.

MODES OF TREATMENT AND PREVENTION

Pastures with a copper content below 4 p.p.m. lead to signs of copper deficiency in ruminants, and pastures containing 7·5 p.p.m. have been regarded as curative and levels of from 20 to 30 p.p.m. in the dry matter of the forage are known to be curative. In Scotland it has been found that a 20 lb. dressing of copper sulphate raised the copper content of the herbage from 2·5 p.p.m. of copper to 30 p.p.m. It is useful to remember that copper deficiency results in Derbyshire where the herbage contains as much as 20 p.p.m. copper.

In New Zealand, for example, uncomplicated copper deficiency can be completely prevented in lambs by either top-dressing the copper-deficient soil (frequently peat) pastures with 5 to 10 lb. $CuSO_4{\cdot}5H_2O$ per acre before lambing begins; giving ewes 16 weekly drenches of 1·5 g. $CuSO_4{\cdot}5H_2O$ from the time tupping begins; 5 drenches of 1·5 g. between the 16th and 7th weeks before lambing; 3 drenches of 2·5 g. between the 16th and 11th weeks before lambing; 2 drenches of 1·5 g. weekly for 8 weeks beginning 7 weeks before lambing; and drenching the lambs twice weekly from birth with 35 mg. in 0·5 oz. solution. More usually in Britain copper is given as a drench of 10 ml. copper solution containing 0·5 g. $CuSO_4{\cdot}5H_2O$ at fortnightly intervals. It is thought by some that the daily allowance for pregnant ewes of 5 mg. per diem is sufficient. The addition of 0·5 per cent of copper sulphate ($CuSO_4{\cdot}5H_2O$) to salt would furnish 10 mg. copper per day. Others have suggested 1 per cent to the salt. Under practical conditions it is rarely found that less frequent dosing gives sufficiently good control. The great practical difficulty in controlling the disease lies in bringing pregnant ewes down from the hills every two weeks. It is interesting therefore to note that in the west of Scotland, DUNLOP has prevented swayback in the offspring of susceptible ewes by administration of 1 g. $CuSO_4{\cdot}5H_2O$ in 30 ml. water per ewe immediately before lambing.

It is difficult to see how the copper works at such a late date in gestation and it is doubtful if such a procedure would be effective in severe copper deficiency. Copper has been given as one shot of 20 mg. $CuSO_4$ to the pregnant ewe by vein about 6 weeks before parturition.

The so-called ' copper pine ' of calves presents some quite distinct features in that only young stock are affected ; clinically there is no anaemia or pica, no skeletal changes, absence of haemosiderosis, and this ' pining ' which can be cured or prevented by small supplements of copper occurs on herbage of apparently adequate copper content.

PIGLET ANAEMIA

Danish workers have found that regardless of copper treatment, pregnant sows at the time of farrowing have higher than normal copper levels and that copper supplements raise them still further. The low serum copper of the newborn piglet is due to the low serum albumin which is 41 per cent of that of the sow and some 90 per cent of the copper of the serum is in the albumin fraction.

The administration of copper to the sow made no difference to the haemoglobin level of the newborn at the time of delivery nor during the next four weeks. Piglets with access to soil or which have received iron salts, *e.g.* reduced iron, pick up enough copper to meet their requirements from these sources unless in the case of the iron salts a highly purified compound is used (*see also* under Iron, page 149).

HORSES

It has been suggested that foals in areas of enzootic ataxia may exhibit malnutrition and abnormalities in structure and position of limbs.

POULTRY

The nutrient allowance recommended by the Committee on Animal Nutrition of the U.S. National Research Council is 0·9 mg. per lb. for growing chicks.

MOLYBDENUM

It is appropriate to discuss the effect of traces of molybdenum at this stage as it appears to affect the availability of copper. This element occurs in traces in all animal and plant tissues and is known to perform an essential function in traces in higher plants, and in certain micro-organisms and there is now evidence that it is necessary for animals as a constituent of xanthine oxidase (De Renzo *et al*, 1953). That molybdenum has a profound influence on the animal is demonstrated by the excessive scouring and symptoms of copper deficiency which arise in cattle and sheep confined to pastures which contain relatively large quantities of molybdenum.

EFFECTS OF EXCESSIVE INGESTION OF MOLYBDENUM BY CATTLE

In central Somerset FERGUSON, LEWIS and WATSON found a considerable area of pasture, probably at least 20,000 acres, which caused scouring in grazing cattle. Smaller areas were also found in South Somerset, Gloucester, Warwick and Lincoln. Such land is known in Somerset as ' teart '. The scouring occurs mainly during the periods of flush growth in spring and later summer. Sheep are less affected and horses not at all.

Where the soils are acid or slightly acid in reaction, the molybdenum in the soil is only absorbed with difficulty by pasture plants; on neutral or alkaline soils absorption of molybdenum by pasture plants is rapid. The addition of acidic substances to ' teart ' soils reduces uptake of molybdenum by the herbage and so reduces its teartness.

Only ruminants, particularly cows in milk and young stock, are affected by such pasture; strong fattening stock, though they may not scour badly are usually unthrifty and do not grow well. Scouring may occur within 24 hours of putting cattle to graze in the pasture. The dung becomes very loose and watery, is yellow-green in colour and bubbly, and has a foul smell. The animals soon become filthy, their coats stare; Red Devon cattle turn a dirty yellow, black beasts go rusty in colour. If left too long the beasts may die or suffer permanent injury. When the animals are removed to a non-' teart ' pasture the scouring soon ceases. Sheep are not so seriously affected but they suffer in a milder way.

All pasture species do not absorb molybdenum with equal ease; leguminous plants, such as clovers, absorb considerably more than grasses, hence the more clover the greater the scouring. The higher the *p*H the greater the uptake of molybdenum. The observation that the diarrhoea, consequent emaciation and depigmentation of the hair are closely correlated with the molybdenum content of the pastures, which ranges from the very high levels of 20 to 100 p.p.m. molybdenum on a dry basis (non-' teart ' pasture less than 5 p.p.m.) and that symptoms of a similar nature could be induced in stalled cattle by administration of relatively large doses of sodium molybdate indicated excessive ingestion of molybdenum as the cause of the malady. When Ferguson and his colleagues were considering the question of an antidote, a paper was published by BROUWER and a group of his colleagues in Holland describing a type of scouring, apparently very similar to ' teart ' scouring, which occurred on a reclaimed polder. The latter suggested that a deficiency of copper might be the cause. Ferguson and his group examined the copper content of ' teart ' and non-' teart ' herbage but found no difference, the copper contents being between 11 and 18 p.p.m. D.M., figures about double those quoted by the Dutch workers. The British workers tested out the effects of giving small quantities of copper sulphate and it appeared that a daily dose of 2 g. copper sulphate was effective in stopping the scouring of dairy cows. In practice the administration of copper sulphate should not be necessary for more than 6 weeks and it is unlikely to cause any physiological disturbance. Ferguson has recently reported that one intravenous dose of 300 mg. copper as copper sulphate in isotonic solution controls scouring in adult cattle for two to four weeks. Half that quantity is sufficient for yearling animals.

The immediate cause of the intense scouring has not been clarified. It may be induced in some but not in all cattle by the addition of sodium molybdate to the normal ration although the quantity of molybdenum that is required in order to be effective in this way exceeds that which is ingested in ‘ teart ’ pastures and it may be controlled without significant influence on the high concentration of molybdenum in the blood by dosing the animals with copper sulphate. Intravenous injection of very much smaller quantities of copper sulphate is reported to be just as effective.

In New Zealand a ‘ teart’-like condition which affects cattle grazing on land reclaimed from peat swamps has been described by CUNNINGHAM and his colleagues and is associated with relatively high concentrations of molybdenum and ‘ normal ’ concentrations of copper in the pastures. The animals become depleted of copper and develop the syndrome of induced copper deficiency. From Florida and California come reports of a similar nature.

THE EFFECT OF MOLYBDENUM ON COPPER METABOLISM

It would seem that ‘ teart ’ is an extreme manifestation of an induced copper deficiency but it is to be noted that an excessive ingestion of molybdenum is not invariably the prime aetiological factor in the induced copper deficiency syndrome. While there seems to be no doubt that the copper reserves in the livers of sheep and cattle may be depleted by dosing the animals with molybdate, there is no doubt that sheep may ingest considerable amounts of molybdate without evincing any sign of deficiency symptoms, although the copper concentration in their livers may become materially reduced. From South Australia there is a report that in an area where the herbage is short of copper and where they invariably develop the uncomplicated syndrome of copper deficiency, the administration of molybdenum equivalent to that ingested from ‘ teart ’ pastures significantly decreased the rate of depletion of copper from the liver and maintained a higher concentration of copper in the blood but precipitated in an acute form the symptoms of copper deficiency. Molybdenum would appear to fix copper in a form that is not utilizable by the tissues or to antagonize the copper-containing enzymes. This phenomenon is apparently not confined to ruminants.

Long-continued treatment with molybdate materially reduces the quantity of copper which is normally transferred to the foetus. Molybdenum passes through the placenta and so the availability of even this short supply of copper may be further diminished. Molybdenum is secreted in the milk and this may still further reduce the copper status. The evidence suggests that where molybdenum in pastures appears to be the agent inducing swayback in lambs it must be in a more potent form than molybdate.

The osteoporosis reported to occur in cattle and sheep grazing in areas where the available fodder contains a relatively high concentration of molydenum is probably due to a selective inhibition of enzymes involved in calcification, the phosphatases are known to be particularly sensitive to the molybdate ion.

MANGANESE

Manganese is present in all plants and animals and is an essential element in their nutrition. It is widely distributed in soils and rocks but usually in small quantities. Extensive manganese-deficient areas have been found in the United States and the ability of a soil to supply available manganese is determined by the state of oxidation of the manganous-manganic system in the soil. Manganese deficiency in plants may be brought about by over-liming a soil having a low content of active manganese. This effect may be overcome by various methods of treatment.

Manganese occurs principally in the liver, to a less extent in the pancreas, but it is also present in appreciable quantities in some other organs and in the skin including hair, muscle and bones. Tissues range in their content from about 0·2 to 4 μg. Mn/g. D.M.

The identification of manganese as an element essential in traces resulted initially from studies by ORENT and McCOLLUM (1931) on rats. This work in its later stages indicated the rôle of manganese in reproduction, for on a diet low in this element sexual maturity was delayed and ovulation became irregular. If conception did occur the young were born weak or dead and their bodies contained much less manganese than those born from mothers normally fed. A slight progressive anaemia not preventable by copper has also been noted. In the male a diet devoid of the element caused a degeneration of the germinal epithelium. Reproductive effects have been produced experimentally in pigs with diets of 0·5 μg. Mn/g. dry matter. Poultry are the most likely sufferers from a deficiency of this element.

A lowering in the content of manganese in the liver probably affects the arginase activity there, for manganese is a constituent part of this enzyme. There is also a lowered ' alkaline phosphatase activity of bone ' in this deficiency. Phosphorylation activity by liver homogenates from manganese and choline-deficient chicks has been increased

41 per cent by manganese, 13 per cent by choline and 70 per cent by manganese and choline.

It has been determined that 0·3 mg. Mn daily is sufficient for the purposes of normal bone, phosphatase and arginase activity but perhaps insufficient for normal growth. Although lactating dairy cows may retain 150 mg. of manganese daily the possibility of a negative manganese balance in dairy cattle is remote. It has been suggested that 6 μg./g. dry matter is sufficient manganese in the diet for reproduction and rearing in the pig.

PEROSIS OR ‘ SLIPPED TENDON ’ IN POULTRY

In 1935 **Wilgus** and his associates produced evidence that manganese is markedly effective in reducing the incidence of perosis, or ‘ slipped tendon ’, a malformation of the leg bones of growing chicks. This condition arises when the tibio-metatarsal joint swells and the tendo Achilles slips out of its groove, putting the leg out of its normal position. Usually there is an accompanying shortening and thickening of the long bone. Manganese deficiency is not the only factor concerned and choline and biotin have been implicated with other possible causes. So far, the symptoms appear to be the same in each case so that all these factors may be concerned with different links in a chain of events, the breaking of any link giving the same final result. In the laying hen a deficiency of manganese upsets the quality of the shell, although the shell itself contains only a trace of the element.

It is said that the high calcium and phosphorus rations normally fed to poultry are a contributing cause of the occurrence of perosis, and that they also aggravate the effect of a low manganese intake on growth. Bone malformations in the form of crooked front legs have also been produced in rabbits by feeding a diet low in manganese. Just how manganese functions in bone formation is not known.

The ubiquitous occurrence of manganese in the animal body suggests a rôle in general cell metabolism as opposed to metabolic processes characteristic of particular tissues. Such a rôle does not exclude other rôles. Manganese may be essential for normal bone formation in mammals as well as essential for the prevention of perosis in chicks and turkeys. The mode of action of this element in calcium and phosphorus metabolism has not yet been established but a rôle as activator of the enzyme phosphatase in bone has been suggested because chicks receiving added manganese show a rise in the manganese content of bone and an increase in phosphatase activity. Analyses have shown that most of the manganese in ox bone is deposited with the inorganic salts, but a small proportion is definitely associated with the organic matrix.

The accumulating evidence on manganese-deficient rats, mice, rabbits, and swine suggests the occurrence of abnormal skeletal tissues which show certain similarities to the well-defined bone deformities in chicks.

Generally bone deformities such as ' crooked front legs ' in rabbits are accompanied by significantly lower values for fresh weight, ash and bone density. The manganese content of the liver is reduced, but no change in blood serum manganese occurs.

The natural forest pastures of Scandinavia and Finland have a high manganese content in their cultivated soils and a disorder in horses called ' forage anaemia ' has been attributed to the excess manganese. Liming reduces the assimilation of manganese by the plant. It is thought that there is a relationship between excess manganese and vitamin B_1 deficiency in horses but the matter is far from clear.

REQUIREMENTS

Quantitative assessments of allowances for farm stock have only been worked out for poultry and these have been established at 25 mg. per lb. (50 μg./g.) of feed for starting chicks and 15 mg. per lb. (30 μg./g.) for breeding hens. These values have been set high enough to meet the possibility of a ration very high in calcium and phosphorus as a result of the liberal inclusion of bone-meal carrying feeds. The needs for pigs are much lower and probably this is true for other farm animals. It has recently been stated that the critical level for growing pigs is between 12 and 20 μg./g. D.M. They could not tolerate a high level of 500 μg./g. Additions of 40, 80, and 160 μg. manganese/g. to a basal ration containing 12 μg./g. for sows during reproduction and lactation gave no significant difference in performance.

A form of rickets in pigs has recently been reported from Norway by SANDSTEDT and CARLQUIST (1951) which is characterized by swollen streaks on the posterior external contours of the hocks. It is stated to be due to manganese deficiency and can be prevented by giving manganese : curative treatment was not successful.

From a survey of the manganese content of commonly occurring feedstuffs it is evident that no manganese supplements are called for, except possibly for poultry, but even here the need for added manganese has not been firmly established.

ZINC

Only one naturally occurring deficiency of zinc amongst livestock has been reported. Our existing knowledge is based on experimental work largely on rats. It is known that zinc is present in the body in greater quantity than copper and to about half the extent of the body's content of iron, and that it is distributed like copper. Its lack has a generalized effect on growth and reproduction. The thyroid, liver and pancreas contain most of the 2·2 g. present, especially the thyroid. Zinc is a necessary factor in the action of the enzyme carbonic anhydrase of the red cells of the blood and other tissues as has been shown by Keilin and Mann (1940). Zinc forms a prosthetic group in this enzyme which facilitates the liberation of CO_2 from H_2CO_3. Excess zinc has been found to cause in rats a microcytic hypochronic anaemia only partially relieved by addition of copper, and a subnormal rate of growth and of fur. When feeding is stopped the store of the element in the body gradually disappears.

A deficiency of both zinc and copper has been reported in the Coonalpyn Downs region of South Australia by Riceman (1950) and the deficiencies in the soil there are being rectified by treatment with zinc and copper sulphates.

Zinc has been found in the pancreas and also in all commercial preparations of insulin. As the zinc content of the pancreas of a diabetic patient is about one-half that of a non-diabetic, it has been suggested that part of the zinc in the pancreas may be concerned with the storage and utilization of insulin.

The amount of zinc in common foods of animals is greatly in excess of any probable need by the body and thus in practice there is no need for steps to be taken to secure its adequacy in the diet.

IODINE

Iodine is a nutritional necessity for animals but is required in very small amount: the mature animal contains less than 0·00004 per cent and more than half of this is in the thyroid gland. Nine years after its discovery in 1811 in seaweed, it was credited with remedial effects in the treatment of various diseases, especially human goitre. The idea rapidly spread that goitre was in fact the pathological sign of iodine deficiency. Seaweed ash was the principal commercial source of the element until about 1870 when iodine was discovered in the vast natural deposits of sodium nitrate ore in the northern part of Chile.

It was in 1895 that Baumann discovered that iodine is a normal and inevitable constituent of the thyroid gland. This at once placed the iodine treatment of goitre on a rational basis and showed that environmental deficiency of iodine is the primary cause of the disease. On Christmas Day 1914 Kendall in the United States of America isolated the crucial iodine-containing compound of the thyroid gland and at the close of the first quarter of the century Harington in the United Kingdom had determined its lowest chemical constitution, devised means for its synthesis, and described the principal chemical inherencies by which it exercises specific physiological activity.

These advances at once raised the whole question of environmental iodine supply in relation to everyday needs of man and beast. Foods and water supplies all over the world were examined.

It was found that the quantities of iodine in foods are as a rule exceedingly small and that very precise methods are needed for its analysis owing to ready contamination.

Many factors determine the amount of iodine in foodstuffs. Soil richness and soil poverty of this element are generally reflected in the chemical quality of the foods grown on them. It is well known that Chilean sodium nitrate—the only fertilizer containing a relatively high proportion of iodine as a natural constituent—doubles or trebles the iodine content of crops.

Marine foodstuffs are the richest naturally occurring sources.

THE THYROID GLAND

This gland in man and in most domesticated animals is bi-lobed and with the pealike parathyroid glands closely attached, lies on each side of the windpipe. It produces an internal secretion which contains the hormone thyroxine. Thyroxine contains 65 per cent of iodine and is an iodine-containing amino-acid present in the protein thyreoglobulin. The thyroid iodine of normal cows is 250 μg. per g. of tissue and about 230 μg. per g. in pregnant animals. If the thyroid fails to develop in early life there is stunting of physical, mental and sexual development, and the basal metabolism is lowered. In adult animals diminished function is characterized by prematuring aging and sluggishness.

The term ' goitre ' includes all diseases of the thyroid gland which are usually associated with an increase in size. The kind of goitre with which we are concerned here is simple goitre arising from iodine deficiency. It is characterized by excessive multiplication of the cells lining the follicles and by disappearance of the colloid within the follicles. It occurs both sporadically and as a local (endemic) disease.

The enlargement that occurs in simple or endemic goitre is a compensatory hypertrophy, that is, an enlargement involving the formation of more tissue in an effort to supply more secretion.

The requirement for thyroxine varies in accordance with the activity of the body functions it controls, and given a fairly constant but barely adequate supply of iodine in the diet simple goitre is most likely to develop during periods of greatly increased need. In farm animals goitre usually shows itself in the young at birth as a result of a deficiency of iodine in the rations of the mother during gestation. The young are born weak or dead, for under these circumstances the mother is not able to supply the foetus with enough iodine. The danger increases with multiple births.

In ruminants any enlargement of the gland is fairly obvious at the time of birth and the animal may have scanty hair or wool. In pigs the most outstanding feature is hairlessness and they are bloated and have thick skins and a pulpy water-like swelling, especially around the shoulders and neck. In the case of foals the only symptom may be extreme weakness at birth. It is reported that the deformation and lameness of joint in polyarthritis are prevented by iodine administration but more evidence is needed. Birds have enlarged thyroids as a result of iodine deficiency.

In general it may be said that animals born alive with deficient thyroid function due to iodine deficiency in their mothers usually fail to survive or remain weak and unthrifty and that no effective treatment has been found once this is definitely established, for a permanent defect has taken place *in utero*, but in borderline cases the thyroid enlargement may disappear with iodine. Although there is no doubt that iodine treatment is effective as a preventive, iodine administration after the goitre has developed may even be harmful.

FACTORS AFFECTING IODINE UPTAKE

Water with a high calcium or magnesium content may affect the uptake of iodine and where the supply is marginal, goitre may result as is apparently the case in the limestone areas of Derbyshire. As long ago as 1769 PROSSER recognized that " Derby neck " was associated with the hard water of limestone regions.

In addition it is known that there may be specific goitrogenic and antigoitrogenic substances in certain foods, particularly the brassica seem to promote goitre production in man. It has been reported that soya beans are goitrogenic to poultry, stepping up their iodine requirement. Thiourea and thiouracil lower thyroid activity.

IODINE PROPHYLAXIS

Animals absorb the iodides of sodium and potassium with extreme rapidity when taken by mouth. Iodine may also be absorbed from the skin and lungs. Crude salt containing traces of iodine has been used for a long time and at present use of it or of iodized salt is general by raisers of livestock in iodine-deficient regions. The use of iodides in the feed of pregnant sows can alleviate and prevent the ' hairless-pig ' malady which has been shown to result from low iodine assimilation and affects both mother and young, the latter more severely.

In Britain the areas where goitre is or was endemic are in order of incidence : Derbyshire, Gloucestershire, Nottinghamshire and Somersetshire—the high incidence counties—with a rather less high incidence in Devonshire, Dorsetshire and Oxfordshire. Certain areas in southern Scotland, *e.g.* Nithsdale, are also areas of high incidence. In Ireland goitre is endemic throughout the South Riding of County Tipperary and in County Antrim.

In the United States of America the goitre areas are primarily in the north-west and in the region of the Great Lakes, but areas occur elsewhere even in some eastern states. Goitre is reported as endemic in parts of Canada, Mexico, central America, Africa, Australia, New Zealand, continental Europe, and Asia. It has been estimated that before iodine feeding was practised in Montana, goitre caused an annual loss of many thousands of pigs. Serious losses of sheep and cattle have been reported from certain areas. These are now overcome by the use of iodine. There are borderline regions in which the iodine intake is little above minimum requirement and where an enlarged physiological demand by an individual may be responsible for occasional trouble.

IODINE REQUIREMENTS

Although iodine is required throughout life to keep the thyroid gland functioning, we do not have specific knowledge of the minimum iodine requirements. The needs of farm stock are greatest during reproduction : goitre is the result of an advanced state of deficiency.

Recommendations for all-the-year-round feeding are usually calculated to ensure that the needs of breeding stock are taken care of in areas where goitre is very common. Iodine over and above that required has no additional value and if administered in excess iodism will result.

The National Research Council of the U.S. National Academy of Sciences allowance for pigs is 0·2 mg. iodine per 1,000 lb. bodyweight. The iodine allowances per lb. of feed for hens by the same organization are set as follows: starting chicks, 0·5 mg. of feed; growing chicks, 0·3 mg.; laying hens, 0·3 mg., and breeding hens, 0·5 mg. These levels should take care of the goitrogenic effect of large amounts of soya-bean-oil meal in rations.

The most effective means of supplying iodine to stock in proper amounts is through its addition to common salt. The recommendation most generally adopted in Britain is one part of iodine in 2,000 parts of salt (0·05 per cent). Some authorities prefer a much higher concentration in their iodized mineral mixtures and for Ayrshire cows have used a mixture containing about three times as much iodine, with what are claimed to be good results. On the basis of the recommendation of the American Public Health Association, iodized salt is now formulated with one part of potassium iodide in 10,000 parts of salt. This is 0·01 per cent of potassium iodide or 0·0076 per cent iodine. The feeding of salt iodized at this level is considered to furnish several times the iodine requirement for pregnant mares, and this level in the salt of sheep, beef, and dairy cattle, is also said to furnish several times the iodine requirement of these ruminants. Observations on actual rations consumed by dairy cows indicate that iodine intakes empirically secured vary from 1·4 to 5 mg. per day and even higher. We must recognize that we still do not know the requirements of iodine and that it is better meantime to refer to allowances that have prevented deficiency occurring.

As the thyroid has a considerable capacity to store iodine it need not be given every day, indeed in children in goitrous areas iodine deficiency has been prevented by feeding iodide at considerably wide intervals.

Where goitre has been noted in the young the feeding of iodized salt during the last three-quarters of the gestation period of the mothers, has given protection in areas where this occurs.

It is useful at this point to note that salt consumption by individual animals varies enormously; an average value is probably 15½ lb. per year for indoor-fed dairy cows in addition to what has been added to their concentrates. If this were iodized with potassium iodide at a rate of 0·05 per cent this would provide approximately 1·5 mg. of iodine per day.

THYROACTIVE IODINATED PROTEIN

Iodinated casein was first prepared in Germany by LUDWIG and VON MUTZENBECHER (1936, 1939) from which thyroxine, the internal secretion of the thyroid, was isolated. This was confirmed in Britain by HARINGTON and PITT-RIVERS. The thyroidal potency of such products was erratic and sometimes very low and at Missouri REINEKE and TURNER (1942) greatly improved the iodination process so that iodinated casein, having an apparent thyroxine content of approximately 3 per cent and a biological activity many times that of dried thyroid gland, can now be produced. Casein is not essential, for various other proteins have been iodinated successfully. Iodinated protein can be incorporated into dairy cattle feeds without loss of potency.

It is now possible to produce varying degrees of hyperthyroidism simply by feeding iodinated casein; a hypothyroid condition can be produced readily by feeding synthetic goitrogens such as thiourea, thiouracil, thiobarbital and their derivatives. This has been reviewed by BLAXTER, REINKE, CRAMPTON and PETERSEN (1949).

Within a limited range the percentage increase in milk yield caused by feeding iodinated casein or its equivalent of L-thyroxine (which can now be synthesized readily) is roughly proportional to the dosage. Fat percentage also increases, the increase usually appearing at lower dosage levels than the rise in milk yield. With the exception of a small and variable decrease in milk nitrogen, no other important alteration has been noted. Thyroid hormone does not appear to be transmitted to the milk so it is considered that the milk is safe.

To avoid loss of body substance through the thyroidal stimulation resulting from treating dairy cows with iodinated casein or L-thyroxine there must be an increase in nutrient intake. If sufficient extra nutrients are supplied to support both the increased metabolism and the increase in production, normal body weights are maintained. It is very important to keep dosage within the physiological range of the cow. Its use during the declining stages of lactation and during periods of milk scarcity might be profitable, but long-term experiments in Britain have shown that what is gained by enhanced milk yield during part of the period of administration is offset by a shorter lactation and the net effect is that no overall increase in milk yield or butterfat is achieved. With the dosage used no ill effects were noticeable after treatment in successive lactations.

Iodinated protein is poorly tolerated during hot weather. It has proved beneficial in improving the libido and fertility in sluggish and inactive bulls and may provide a means of extending the period of usefulness of some herd sires. It has also been found to overcome summer sterility in rams.

So far, conclusive evidence on the lactation of sows has not been obtained. It is said to increase the growth rate and economy of gain of young growing pigs when given within what is a narrow critical range. Such pigs are said to be thicker bodied, more mature and more uniform in conformation.

In chickens iodinated protein consistently causes a pronounced acceleration of feather growth : its effects on body growth are variable. Small amounts given continuously in the ration have been reported to prevent partially the summer decline in egg production and also to retard the yearly rate of decrease in egg production with advancing age, but more research is needed in this field to assess its rôle in egg production, particularly in view of its effect on the overall lactational performance of dairy cows.

Through its thyroid-inhibiting property thiouracil will cause a depression of milk and egg production, and when given to very young animals will cause growth stasis and varying degrees of cretinism. When given only during the last three to four weeks of the fattening period in chickens and turkeys, and in the last four to six weeks to pigs, this drug caused significant improvement in the economy of gains, in most cases with little depression in the rate of gain. Increased fat deposition has usually been noted in poultry but not in pigs.

FLUORINE

Fluorine is widely distributed in soils and waters: its association with phosphate minerals is particularly significant in plant and animal nutrition for it is considered that fluorine contributes to the insolubility of phosphate deposits and seems to be essential to their preservation in the soils. Although fluorine is widely distributed in communal water supplies throughout the world, no general survey for any one country except the United States has been made. Indeed most of our information comes from that country though on the toxicity side there are carefully documented cases reported in the literature of the United Kingdom.

Plants grown in soil or water containing fluoride do not readily take this up but the absorption by plants is greater from acid than from other soils and hence is decreased by liming.

Although it has not been shown clearly that fluorine is an essential nutrient for adult animals, this may be so, and there is evidence that when optimal amounts are available during growth there is increased resistance to dental caries.

Forage crops may become grossly contaminated from gases and dusts containing fluorine, originating from certain industrial processes. Contamination of crops with fluorine-bearing soil in areas containing deposits of fluorspar and phosphate rock is also a possibility. At least one case of a naturally occurring organic fluorine compound (fluoracetate) in a plant has been found. This shrub is Dichapetalum (Chailletia) cymosum (Hook) Engl. indigenous in South Africa and renowned for its extreme toxicity.

EFFECTS OF FLUORINE

Moulton (1946) stated that in low concentrations in drinking water fluorine exerts a favourable effect on dental health in preventing and arresting dental decay, and for human purposes several countries have taken or are taking steps to raise the level of the drinking water of their populations to a level of not more than 1 to 1·5 parts per million.

It is not proposed here to deal with the effects of acute fluorine poisoning but with the possibility of chronic fluorosis, for that is the intoxication most likely to occur in practical agriculture. This may vary from unsightly mottling of the teeth to gross skeletal change.

THE FLUORINE HAZARD TO LIVESTOCK

The hazard to farm animals resulting from the ubiquitous occurrence of fluorine in feed and water supply arises largely from the use of fluorine-containing minerals as supplements to farm rations and from industrial fumes and dusts. This whole question has recently been discussed by **Mitchell** and **Edman** (1952). These fluorine-containing minerals are the different varieties of phosphate rock, the superphosphates produced from them as well as the partially defluorinated phosphates and the phosphatic limestone. Phosphate rock contains from 3·25 to 4·0 per cent of fluorine and in the manufacture of superphosphate from phosphate rock, from one-fourth to two-thirds of the fluorine is driven off by volatilization as hydrogen fluoride or as silicon tetrafluoride. Commercially defluorinated phosphates generally contain less than 0·5 per cent fluorine and may contain less than 0·1 per cent, being comparable to bone-meal in this respect. In the case of defluorinated phosphates (not yet made in Britain) the fluorine content has been reduced to amounts that are innocuous over the usual feeding period for meat-producing animals. Here it is a problem of how far calcination and fusion processes may render more available to animals the fluorapatite in the original rock.

Analyses of phosphatic limestones indicate that fluorine is there in proportion to the amount of phosphorus present and although non-phosphatic limestones contain fluorine, the amounts are relatively small unless there is an admixture of fluorite (CaF_2) which occurs in some limestones.

When the fluorine content of the drinking water attains levels of several parts per million it may contribute significantly to the fluorine hazard and it is noteworthy that mottling of the enamel of the teeth of cattle in western Texas has been traceable to the drinking water and, in Australia, chronic endemic dental fluorosis has been observed in sheep that drank water from two artesian bores, one containing 19 and the other 5·6 p.p.m. of fluorine.

The production of acid phosphate and defluorinated phosphate, the electrolytic production of aluminium, the manufacture of bricks from fluorine-bearing clays, the calcining of ironstone and certain enamelling processes, have been the chief industrial hazards involved. Even coal and shales associated with coal contain fluorine in amounts ranging from 40 to 50 up to several hundred parts per million, so that even coal-burning furnaces may constitute a hazard under certain conditions. Probably the most complete reports on industrial hazards to stock are those described for cattle in the neighbourhood of the aluminium works near Fort William. Detailed accounts of the effects of such conditions on livestock are given in reports by BOSWORTH and his colleagues (1941) and subsequent workers.

Hydrofluoric acid is the main hazardous product present in the fluorine-bearing fumes arising from factories processing fluorine-containing ores, and the fluorine-bearing dust may consist of fluorides, such as sodium fluoride or cryolite, which have been volatilized and then condensed in the cold surrounding atmosphere. The leaves of plants may absorb the gas and collect some of the dust on their surfaces. Green observed an extremely high concentration—2,000 p.p.m. D.M. in grass near ironstone-calcining mounds, and about 300 p.p.m. D.M. on a straw stack a mile away. Fluorine has been noted to the extent of 1,100 p.p.m. on a dry matter basis in vegetation a quarter of a mile from an aluminium reduction plant emitting fluorine fumes. In certain areas of the world phosphatic dust may bring its quota of fluorine. Fluorosis has been experienced in Iceland during and after volcanic eruptions and cattle may suffer severe intoxication.

The toxicity of inorganic fluorine compounds depends to some extent on their solubility in water above certain minimum levels of intake. Sodium fluoride and sodium fluorsilicate are the most toxic and calcium fluoride is the least toxic among the compounds studied on the laboratory rat. The fluorine in cryolite and in rock phosphate and its processed derivatives is intermediate in toxicity, but its relative toxicity from these two sources has not been clearly distinguished. According to Mitchell and Edman the evidence indicates that the fluorine of sodium fluoride, up to levels that will affect the appetite and growth of animals, is about twice as toxic as the fluorine of cryolite and, presumably, of rock phosphate. The level of fluorine as rock phosphate which is on the borderline of toxicity for cattle, sheep, and pigs is about 0·01 per cent, or 100 p.p.m., of the total dry ration. In the case of chicks the level is higher, about 0·035 per cent, and for laying hens higher still, namely 0·053 per cent. It is to be noted that the values for chicks are based on relatively short periods of feeding.

Degenerative tooth changes develop in cattle and sheep at a level of 100 p.p.m. fluorine in the dry ration the source being rock phosphate and take from 3 to 5½ years to appear, but the damage in that time is apparently not sufficiently serious to impair appetite, general health, and in the case of females reproduction and lactation. The same seems to hold for pigs though the periods of observation have generally been less than one year.

As far as the economic life of the animal is considered, as it must be with breeding animals, the permissible level of fluorine in the total air-dry ration as rock phosphate or its derivatives should be reduced to about 50 p.p.m. for cattle and sheep. If, however, sodium fluoride or other very soluble compound be the source then the borderline level of toxicity would need to be reduced by about 50 per cent according to available evidence, namely to 50 p.p.m. for non-breeding animals and to half this for breeding animals. Under such circumstances contamination from the industrial fumes and dusts to the extent of 25 to 50 p.p.m. of fluorine on the dry basis may result in fluorosis in grazing breeding animals.

SIGNS OF CHRONIC FLUOROSIS IN LIVESTOCK

Clinical.—The chief sign in cattle is lameness usually associated with marked skeletal abnormalities. Enlargement of the breast bone and lower jaw is often found and there is invariably an increase in the small bones of the feet. Pressure on the affected bones causes great pain. Well-defined protuberances or callosities of bone occur and often extend over a considerable portion of the shafts of the long bones. Appetite is impaired and the animals often become unthrifty and emaciated. Mottling of the permanent incisor teeth is a constant finding in cattle reared in a contaminated area. These teeth may become deformed and brittle. The molars show poor wearing quality. Erosion results if there is continued ingestion of fluorine in large amounts. In many cases the formation and eruption of the teeth are so irregular as to lead to deformity of the mouth and this with the irregular wear produces a state of the teeth that renders it impossible for the animal to chew its food properly. Infection may lead to an alveolar periostitis and suppuration of the roots of the cheek teeth, and this in turn may lead to infection of the adjacent cavities of the skull. Most of the ingested fluorine retained by animals is deposited in the bones and teeth. In animals not unduly exposed to fluorine, the ash of bones generally contains 0·01 to 0·15 per cent of fluorine, somewhat more than in ash of the teeth.

It has been found that the presence of fluorine in the ration increases the concentration of iodine in the thyroid glands of lambs under conditions of both adequate and inadequate iodine intake, in proportion to the fluorine given per unit of bodyweight.

THE FLUORINE CONTENT OF PRODUCTS FROM FLUOROTIC FARM ANIMALS

According to Cohrs (1941) the muscle and viscera of animals suffering from fluorine poisoning will contain more fluorine than the meat from animals not so afflicted, but the raised fluorine levels amounting to only 2 or 3 p.p.m. on the dry matter basis, are still so low as to constitute no appreciable hazard to the consumer.

Raising the fluorine content of the cow's ration to relatively high levels does not raise the level of fluorine in the milk appreciably. In severe fluorosis the fluorine content of cow's and ewe's milk has been raised but not highly.

Unlike milk, eggs may exhibit appreciable amounts of fluorine if the hens are consuming a ration containing from 1 to 3 per cent of rock phosphate. It appears mainly in the yolk.

ARSENIC, LEAD, MERCURY AND SELENIUM

So far as is known these four elements are not essential to plants and animals and are poisonous to both in rather small quantities. The extensive use of lead arsenate in insect and weed control and the more recent use of selenium as an insecticide have raised important issues regarding their fate when added to the soil and their possible influence on plants and on animals feeding on plants. Poisoning of stock may occur from grazing pastures or fodder contaminated with arsenic-containing flue dusts from smelting works. In the United States, notably in some areas of the plains of South Dakota, selenium has been found to be responsible for a peculiar disease of livestock, and is known locally as ‘ alkali disease ’ or ‘ blind staggers ’.

ARSENIC

Lead arsenate is widely used for spraying apples, pears and other fruit as a protection against several different species of caterpillar, particularly that of the codlin moth, no alternative having yet been found. Lead arsenate is partially converted by weathering into a basic lead arsenate with liberation of soluble arsenic acid so that arsenic decreases more rapidly than the lead. As stock may graze orchards there is the chance of poisoning. It is now customary to exclude animals for some time after spraying.

The toxic action of arsenious oxide has been shown to be due to its combination with thiol compounds in the body with the formation of thioarsenates. It interferes therefore with enzyme systems which depend upon these thiols for their operation. Arsenic acid and arsenates do not react with thiols and are in consequence not acutely toxic until reduced in the body to arsenious acid or arsenites. Arsenates are in general eliminated much more readily by the kidneys than are arsenites. It would be expected that arsenates would be less toxic at high levels of intake than arsenites, but that at low levels reduction to arsenite might be sufficiently rapid and complete to eliminate any difference in toxicity. The relative insolubility of some arsenic compounds in the digestive tract may also affect toxicity. Insoluble lead arsenate has been stated to be relatively less toxic on this account, although it is an effective insecticide (MONIER-WILLIAMS, 1949).

The addition of lime to decrease the acidity of the soil or the application of hydrated ferric oxides or ferric sulphate, appears to be the most practical remedy where contamination has occurred. GILBERT (1948) states that there seems to be no danger to animals which feed on vegetation from soils high in arsenic, as the plants will be injured before accumulating enough to be toxic to the animals. Such a statement requires careful scrutiny and very careful check. WILLIAMS and WHETSTONE (1940) state that the amount taken up from the soil, even when highly charged, is negligible. In general, arsenates in soil are much less toxic than arsenites. Normal soils may contain 0·3 to 38 p.p.m. arsenic (as arsenious oxide).

Toxicity.—Spraying fruit trees with arsenicals may have a serious effect on bees. Bees killed with arsenic contained 1 part per 45,000 parts of dead bee. The lethal dose is about 2 μg. The honey is said not to contain significant amounts.

The minimum fatal dose of arsenious oxide is about 15 mg. per kg. body weight. Chickens are stated to be particularly resistant. Dosage at 2 mg. per kg. bodyweight is slightly toxic to rats.

LEAD

Though present in measurable quantities under 'normal' conditions lead in the diet is not a nutrient but constitutes a potential hazard. It is present in plants and soils in very small amounts and under ordinary circumstances the quantity consumed by animals has no effect on health. Its effects are, however, cumulative in that repeated doses, each of which is far too small to produce any appreciable effect on health, may in course of time cause serious injury. About six times as much lead is excreted in the faeces as in the urine and in the case of man whose total intake per day in towns is probably 0·4 mg. from all sources, about as much is inhaled as dust as is excreted in the urine.

Lead tends to accumulate in the bones. Flat bones contain more than long bones, the ends of the latter more than the shafts. As much as 1.5 g. of lead (100 μg./g.) have been found in the skeleton of an apparently normal man; but lead stored in bone is not necessarily inert. Any condition which favours decalcification, *e.g.*, lactation or starvation, will also favour its release, especially where there is a deficiency of calcium and phosphorus in the feed.

To exert its full toxic effect, lead must reach the systemic blood, and the lead content of blood is therefore the best index of lead poisoning. The toxic action of lead in the bloodstream is characterized by anaemia. It does not accumulate to any great extent in the liver, kidneys, or other organs, although this may happen in chronic plumbism.

Milk is one of the best antidotes for lead poisoning. The calcium: phosphorus ratio in the diet and also the absolute amount of calcium there appear to play a part, lead absorption being low on high calcium diets, and *vice versa*. The question whether and to what extent food interferes with the intestinal absorption of lead is of great importance.

Lead is ‘ fixed ’ by the clay of the soil; and it would appear that the sulphate, sulphide, phosphate and carbonate ions would render lead added to a normal soil so insoluble as to be inactive. Very acid soils, *e.g.* peaty soils, increase the solubility of lead. Most outbreaks of lead poisoning arise from the action of acid peaty water on lead pipes, the eating of lead-containing paint and the contamination arising from the use of lead compounds in orchards.

MERCURY

Mercury in traces is widely distributed in nature in rocks, soils, dusts (especially soot), water, etc., and occurs in traces therefore in nearly all foods.

Mercury is highly fungicidal and gives effective means of control of a number of plant diseases at extremely low concentrations. Its use on brassica seedlings in the form of mercurous chloride or as a very dilute solution of corrosive sublimate, involves no consumer risk. Organo-mercury compounds as dusts have achieved great success in controlling certain seed-borne diseases of cereal and other crops, and much interest has recently been taken in their application as sprays to fruit trees for the control of scab. A problem which crops up is whether grain treated with an organo-mercury seed dressing and left over after sowing, may be fed to poultry. In grain treated with organo-mercury preparations levels of 2 to 25 p.p.m. of mercury have been found. This grain fed to small animals produced slight toxic effects only after long periods of feeding. 0·07 mg. of mercury in the form of mercury-treated grain given daily to rabbits for 3 months did them no harm, and fertility was unaffected. The minimum toxic dose for rabbits lies between 2·3 and 5 mg. mercury daily when administered over a period of 5 months.

Edwards (1942) has recorded a case of fatal poisoning of a horse through eating treated grain. Wheat grown in districts where mercury treatment of the seed is practised has been found to contain 0·016 to 0·031 p.p.m., a negligible quantity according to Monier-Williams (1949).

SELENIUM

Selenium has a toxic effect upon animals comparable with, if not greater than, arsenic, giving rise to somewhat similar symptoms.

Selenium is the only mineral element known at present which under natural conditions may be dangerously toxic to animals. Selenium is toxic to many plants but certain species seem to be selenium accumulators on seleniferous soils and are able to absorb many times the amount that would be lethal to ordinary plants. TRELEASE (1945) states that the average selenium content of these accumulators, almost all of which are legumes in the genus astragalus, is about 800 parts per million dry matter, and the highest is 15,000 parts per million. In contrast wheat from the same soils averaged less than 5 parts per million of selenium. Seleniferous soils are widely distributed over the semi-arid regions of the western half of the United States—in particular South Dakota, Wyoming and Nebraska, where the rainfall is insufficient to leach out water-soluble selenium compounds.

An acute and a chronic form of poisoning have been reported, both of which are characterized by the same general form of disorder. In the acute form of the disease, ‘ blind staggers ’, prevalent in Wyoming, the animals become blind and suffer from muscular weakness and apathy, accompanied by congestion of the lungs, haemorrhages and convulsions. In the chronic form, ‘ alkali disease ’, predominant in South Dakota, the symptoms are wasting, loss of hair from mane and tail, and an inflammation and deformity of the hooves characterized by a ring appearing on the wall of the hoof below the coronary band and in more advanced cases the hoof gradually separates and may slough off. Colts are sometimes born with deformed hooves. Chronic selenium toxicity occurs when horses consume feed containing from 5 to 40 μg. of selenium per gramme dry basis.

It was FRANKE (1934) who showed that the cause was a toxic substance in the grain grown in these areas, and he identified it as selenium, an element which NELSON, HURD-KARRER and ROBINSON (1933) had already found to be absorbed by wheat and other crops from soil and from insecticidal spray residues, and to be extremely toxic to laboratory animals. The toxicity of selenium is reported to be markedly reduced when the diet contains a high proportion of protein, and arsenic compounds also tend to protect animals against its toxic action. Some insects are very sensitive to selenium and are killed by concentrations in the plant so low that they do not injure the leaves or other organs.

So far it is only in lower animals, horses, cattle and pigs, that the occurrence of selenium poisoning has been fully proved.

SELENIUM IN THE SOIL

Selenium occurs generally in soils derived from cretaceous pyritic shales, especially in districts of low rainfall. It exists in these soils chiefly as basic ferric selenite, calcium selinate and organic selenium compounds derived from decayed plant tissue. The amount of selenium in the affected soils ranged from traces up to 12 p.p.m. but in most of these localities from 1 to 3 p.p.m. with occasional soils containing up to 30 p.p.m. Selenium is removed from the soil by rain and irrigation and toxic soils are found only in dry climates. They occur in Mexico, Argentina, Chile, Peru, China, and probably elsewhere.

Selenium, molybdenum and vanadium are all absorbed by plants ; tellurium has been found only in a few native plants in Wyoming. Only the two first named, selenium and molybdenum, have so far been found to be taken up in amount sufficient to poison animals. Plants have been divided roughly into three classes according to their capacity for taking up selenium : (1) Those which absorb it readily and grow best on seleniferous soils. There are about thirty of these, mostly perennial plants of the orders leguminosae, cruciferae and compositae. (2) Plants which can absorb moderate or even large amounts without severe injury (wheat, barley, oats, maize, rye, onions). (3) Plants showing a limited tolerance for and absorbing only slight amounts (up to 5 p.p.m.) when grown on seleniferous soils. To this class belong many grasses and most garden vegetables.

Plants of the first of these classes seem to thrive only upon soils containing selenium and absorb relatively enormous amounts of it. Some species of vetch (astragalus) can take up over 4,000 p.p.m. These have been called ‘ indicator plants ’ since their presence indicates that the soil is seleniferous. These plants differ from most plants in that they can take up the selenium from inorganic compounds in the soil. Their growth and decay results in the accumulation of organic selenium compounds which can be absorbed by other plants.

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ENVIRONMENT

CHAPTER 5

THE ECOLOGY OF DOMESTICATED ANIMALS

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ECOLOGY has been defined as that branch of biology which deals with the relations of living organisms to their environments, their habits and their modes of life. In regard to domesticated animals any discussion of ecology must also clearly include their relationships to human society and economy, and in particular their productivity. The study of animal ecology as a separate science is itself of relatively recent origin (ALLEE *et al*, 1949), and its application to domesticated stock is still fragmentary and unsystematized. Yet, as will be shown later, as long as one hundred years ago BERGMANN and others had enunciated general principles relating form to function in animals inhabiting widely different areas and had in many instances applied these principles to domesticated species. It is only within the last two decades that this earlier work on livestock has been re-developed and expanded, notably by RHOAD, BONSMA, BISSCHOP, KELLEY, FRENCH and others. Even so, a systematized science has not yet been fashioned; our slightly less than sparse knowledge is still largely uncorrelated and unorganized.

The purpose of this chapter is to bring together into a consistent story the widely scattered facts regarding form and function in domesticated animals which have now become available, and to relate these on the one hand to the earlier enunciated principles and on the other to the newer physiological conceptions of heat tolerance and climatic adaptation. It is inevitable that such a synthesis of old and new should be both speculative and at times dogmatic, that much of the material should be descriptive and much of the discussion open to attack as being teleological in outlook. Moreover, clearly with such an approach the subject matter cannot be limited solely to recent advances; much of the discussion must be based not only on far earlier work but equally on the author's own material and views. This is inevitable in the development of any new branch of science.

It has been felt logical to preface this chapter with a brief description of the extent to which animal domestication has proved possible and a summary of the geographical distribution of the present domesticated species. This will be followed by a discussion of the general principles governing form and function, and by illustrations of these principles drawn from existing types of livestock. Finally, based on these general principles, methods will be described of determining the suitability of livestock for introduction into new areas (a practical problem of great importance to world livestock improvement) and some typical results of such introductions (and the lessons to be learnt from them) will be discussed.

THE EXTENT OF ANIMAL DOMESTICATION

HUNTINGDON (1925), in a pioneer survey of the world distribution of domesticated animals, listed only thirty as being of substantial economic importance. Of these, two (the bee and silkworm) are insects, nine (the hen, turkey, duck, goose, swan, guinea fowl, peafowl, pigeon and ostrich) are birds, and three (the dog, cat and rabbit) are small mammals of very limited utility. The remaining sixteen mammals constitute by far the most important classes of domesticated livestock. They comprise the following:

Equidae:	horse, ass
Camelidae:	Arabian and Bactrian camels, llama and alpaca
Bovidae:	European and zebu* cattle, buffalo, yak, gayal, banteng, sheep and goat
Cervidae:	reindeer
Suidae:	pig

Huntingdon stressed the very limited length of this list in view of the fact that the world's mammals include over three thousand species, and he implied that the qualities necessary to domestication are sparsely distributed. Such qualities include tractability and docility (in the sense of aptness to training and to management), possession of the herding instinct, for certain purposes (*e.g.* riding) a high degree of intelligence, and from the more purely ecological aspect certain special potentialities for a symbiotic life with man. Among these the three most important are ability to sustain life in man's environment or on the by-products of his agriculture (for this reason most domesticated animals are herbivores), a high degree of adaptation to fairly wide variations in environment (usually through the development of localized types or breeds), and a capacity for specialized functional development, notably in locomotion (for riding, transport or draught), in rate and form of growth (for meat, wool, hides and skins) and in mammary development (for milk).

While such a combination of qualities and potentialities is hardly likely to be common, it would be wrong to regard the very limited list of currently domesticated animals as necessarily exclusive.

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* Commonly but incorrectly termed 'Brahman' cattle in North America, from their Indian origin.

Although the origins of domestication are prehistoric, an examination of the sources of our present livestock shows that domestication itself is an invariable accompaniment of a relatively high level of human culture. Thus the domesticated breeds of cattle, sheep, goats, pigs and horses originated either from the older civilized areas of Central, Southern and Western Asia or of Europe, while the ancient cultures of Arabia and North Africa furnished the ass and the Arabian camel. In the absence of the natural progenitors of these European and Asiatic species, the equally ancient Inca civilization of South America produced the domesticated llama and alpaca, animals ecologically suited to the Andean and Peruvian environments. On the other hand the aboriginals of North America and Australasia, whose agriculture never developed beyond the most primitive cultivations and whose food and clothing were largely furnished by the hunting of wild animals, failed to produce any domesticated species although (to take an obvious example) the North American bison was at one time widely distributed throughout that sub-continent (NEWBIGIN, 1936) and was probably no wilder than the original European and Asiatic cattle. In consequence, as seems inevitable in all human migrations, the subsequent development of less primitive methods of food production by immigrants from the Old World was accompanied by widespread introductions of exotic species of domesticated livestock from Europe and Asia. As FRASER (1953) has so aptly suggested, had the Incas achieved world empire instead, we might, today, have found llamas in Northumberland and alpacas on the Grampian hills! From the ecological aspect this is a point of major significance; the fact that North America was populated primarily by British livestock breeds and South America by breeds of predominantly Spanish origin was due mainly *not* to the fact that such breeds were ecologically suited to their new environments but to the fact that, lacking any local domesticated animals, the immigrants brought those which were most readily to hand and which had proved their value in their home environment. The dangers of such a haphazard approach to livestock introduction will be referred to later in this chapter.

THE DISTRIBUTION OF DOMESTICATED ANIMALS

Although the world's domesticated animals cover such a limited range of species, the actual numbers of domesticated livestock are very large. Representative figures are shown by continents in Table 5.1, side-by-side with the equivalent land areas and human populations (F.A.O., 1950a). Since, subject to the proviso in the previous paragraph, the distribution of such livestock should furnish at least a rough indication of their suitability to the various continents and thus indirectly to the various climatic regions, this table will provide a useful introduction to the present study.

TABLE 5.1

POPULATION AND DISTRIBUTION OF DOMESTICATED ANIMALS BY CONTINENTS (1935–39)*

	Area†	*Human*	*Buffaloes*	*Camels*	*Total*‡ *Equines*	*Horses*	*Asses*	*Goats*	*Sheep*	*Cattle*	*Pigs*	*Poultry*
A. *Population* (*in millions*)												
Europe	490	370	½	§	25	20	3	25	119	102	78	780
U.S.S.R.	2,220	190	§	½	18	17	½	9	57	63	31	230
Asia	2,690	1,140	74	2½	33	13	15½	123	126	228	85	650
Africa	3,040	170	1½	6	13	3	8	65	108	76	3	120
North and Central America	2,430	180	—	—	25	17	3	12	62	101	63	570
South America	1,780	90	—	—	24	18	4	15	97	106	30	150
Oceania	850	10	§	§	2	2	§	§	143	18	2	20
World Total	13,500	2,150	76	9	140	90	34	249	712	694	292	2,520
B. *Percentage distribution*												
Europe	4	17	1	§	18	22	9	10	17	15	27	31
U.S.S.R.	16	9	§	4	13	19	2	4	8	9	10	9
Asia	20	53	97	28	23	15	45	49	18	33	29	26
Africa	23	8	2	68	9	3	23	26	15	11	1	5
North and Central America	18	8	—	—	18	19	9	5	9	15	22	22
South America	13	4	—	—	17	20	12	6	13	15	10	6
Oceania	6	1	§	§	2	2	§	§	20	2	1	1
World Total	100	100	100	100	100	100	100	100	100	100	100	100

* Figures obtained from F.A.O. (1950a). Since the current figures are incomplete those used in this table refer to the period 1935–39, supplemented by any additional returns for countries which had not previously furnished detailed livestock returns. Three species are excluded from the table owing to their extremely limited distribution. These are *reindeer*, of which there are estimated to be a total of about 3 million, which are confined to the extreme northern latitudes of Europe, Asia and North America, and the *llama* and *alpaca*, of which there are about 5 million which are only found in the high plateaux of South America. The *yak*, *gayal* and the *banteng* are included in the figures for cattle or buffaloes.

† In million hectares. ‡ Includes mules. § Indicates less than 100,000 or less than 1 per cent.

In interpreting the table it is, however, necessary to refer briefly and in very broad outline to the two main climatic factors, *i.e.* temperature and rainfall, which, either through their effects upon the animal itself or through their indirect effects on its plant sustenance, must be expected to exert the greatest influence on its distribution.

It is well known that from the equator to the poles the mean annual temperature decreases by about 1°F for each degree of latitude. Thus (as will be seen from *Figure 5.1*) the mean temperatures at the equator and in the tropics lie between 80° and 85°F; in the warm temperate (or sub-tropical) regions between 60° and 70°F, in the cool temperate regions around 50°F, and in the extreme arctic and antarctic well below 40°F. These differences in horizontal temperature stratification are modified by variations in elevation, since the mean temperature also falls by about 1°F for each 300 ft. in altitude. Thus in the Highlands of East Africa which, though close to the equator, are 6,000 to 8,000 ft. above sea level, the mean temperature lies between 60° and 65°F—20° or so below that in the adjacent plains—while in the Andean Plateau of South America, at elevations of 9,000 to 12,000 ft., it may fall to as low a mean as 50°F.

Superimposed on temperature is the effect of rainfall. The factors governing precipitation are complex, and for a detailed discussion reference should be made to such a standard work as that by MILLER (1947). In considering the broad ecological distribution of livestock it is sufficient to note (as shown in *Figure 5.2*) that the incidence of rainfall may vary from over 80 in. in the hot-wet areas of the tropics to under 10 in. in the main desert areas of the world*.

In the light of these broad climatic generalizations the distribution of domesticated livestock shown in Table 5.1 may now be considered.

The first outstanding feature is that certain species are extremely limited in their geographical distribution. Thus the *reindeer* is confined to a relatively narrow belt in the extreme northern areas of Europe, Asia and North America (JACOBI, 1931), where the mean annual temperatures may lie between 10° and 30°F. Although these mean values are well below those required for plant growth, sustenance is available to the reindeer partly because the summer temperatures rise to unexpectedly high levels (in some areas to between 60° and 70°F) and partly because reindeer herd owners are essentially nomadic and are thus able, by extensive southward movements, to avoid the extremes of winter cold (FORDE, 1946). The *llama* and *alpaca* are also very limited in their distribution, being cold resistant types acclimatized to the elevated plateaux of South America (PHILLIPS, 1948). *Buffaloes*,

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* It should be noted, however, that the essence of a desert climate is neither its total precipitation, nor its high temperature (in the Mongolian deserts winter temperatures fall below zero), but the seasonal distribution of the rainfall in such a way as to produce long periods of drought and therefore lack of herbage.

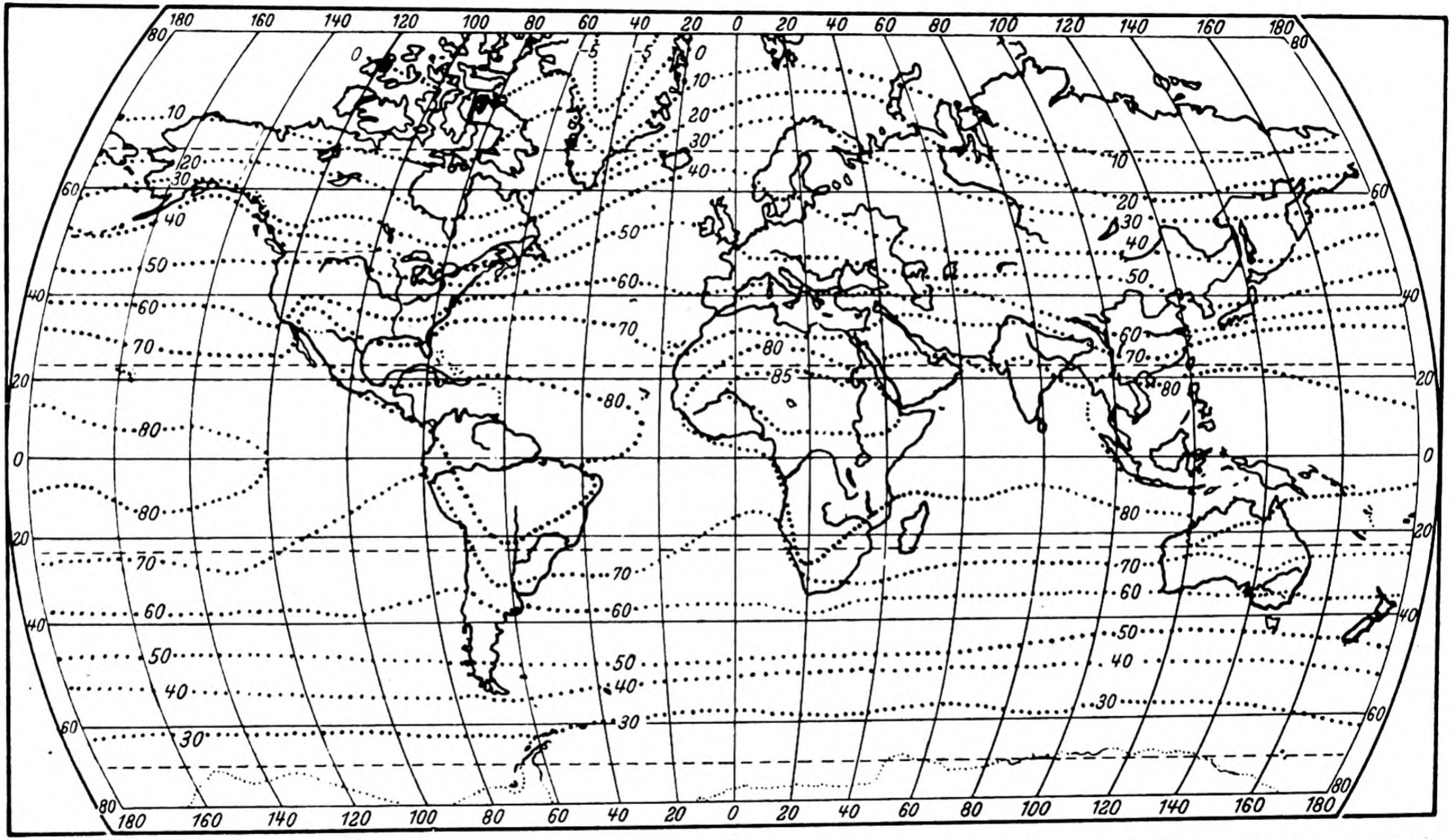
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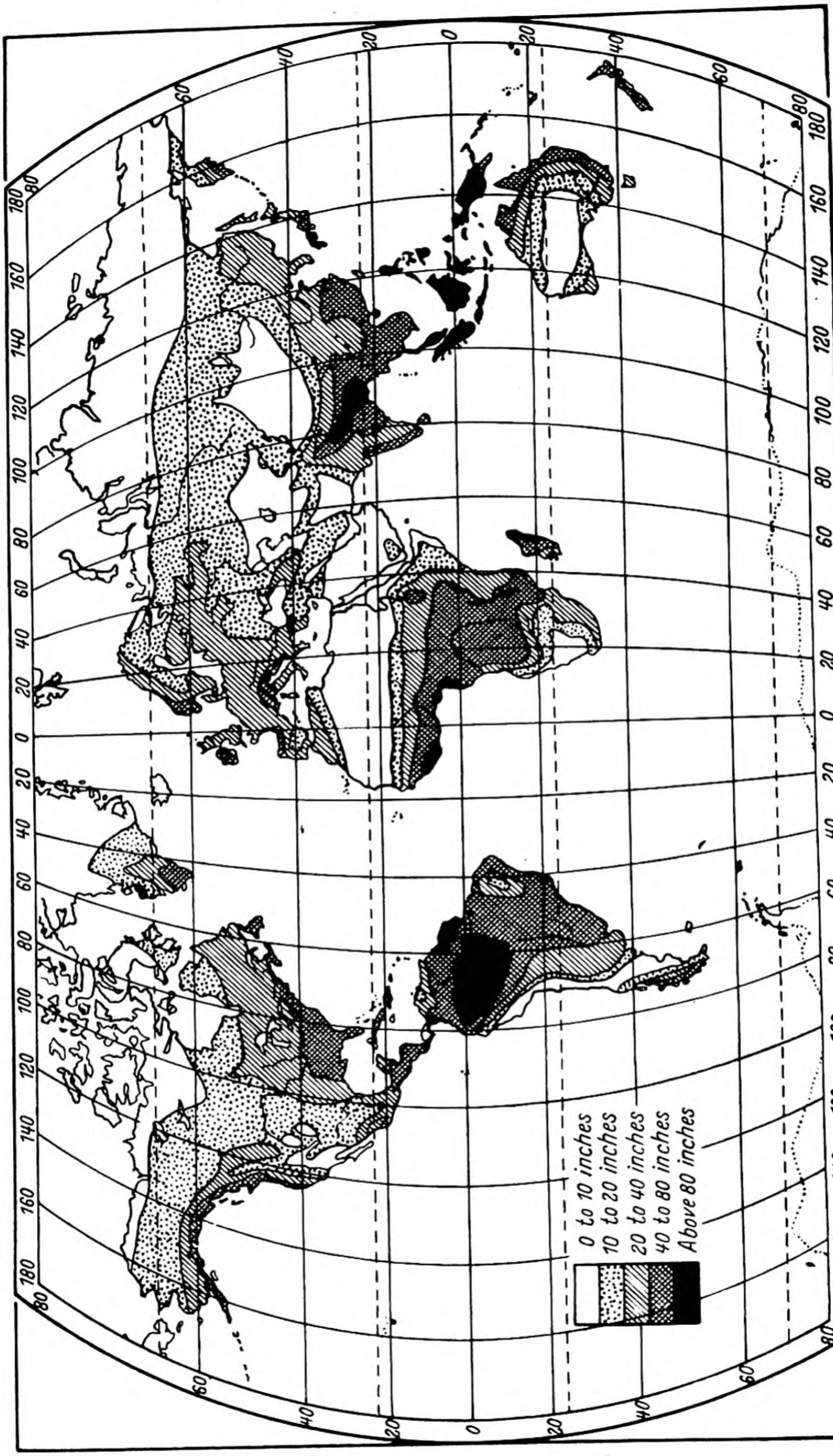
Figure 5.1. Mean annual temperatures at sea level (°F). (From *Weather Elements* by Thomas A. Blair. Copyright 1942 by Prentice-Hall Inc., New York. Reproduced by permission of the publisher.)


0 to 10 inches
10 to 20 inches
20 to 40 inches
40 to 80 inches
Above 80 inches
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180

Figure 5.2. Mean annual precipitation (inches). (From *Weather Elements* by Thomas A. Blair. Copyright 1942 by Prentice-Hall Inc., New York. Reproduced by permission of the publisher.)

which also show a rather wider geographical distribution, are on the other hand almost exclusively confined to the hot-wet areas, notably those associated with rice production. Where they have spread to drier regions, they are almost invariably associated with large-scale irrigation developments in the hotter countries, notably in the Nile Delta of Egypt, the riverain areas of the Tigris and Euphrates in Iraq, and the irrigated plains of the Balkans.

In contrast, the geographical distribution of the *camel* extends over a relatively wide range of both hot and cold desert and semi-arid areas. Though Table 5.1 shows that by far the highest proportion are found in Africa (two-thirds on the south-east borders of the Sahara) large numbers are also found in Asia. These latter are partly the single-humped camels of the hot Arabian deserts and the dry plains of Northern India, but partly the two-humped Bactrian camels inhabiting the colder northern Asiatic deserts. The camel may thus be taken as typifying an animal which owes its relatively wide geographical distribution to specific regional (and hence climatic) differences in form and type. Such regional differences are also broadly revealed in the figures for *equines*. Although the *total* equine population is, as shown in Table 5.1, widely distributed, the proportion of *horses* is far higher in those continents which have a cooler and more temperate climate (though, as is well known, there are still wide variations in type and breed within these localities), while in the hotter and more arid areas the *ass* predominates. This is not only clear in relation to the continental figures for Asia and Africa (its origin and natural habitat); on examination of the detailed figures for individual countries, it is found to be no less applicable within the equine populations of the other continents. Thus in both North and South America nine-tenths are found within the borders of the tropics, while even in Europe all but one-fifth are found in countries bordering on the Mediterranean (F.A.O., 1950a). It is clear that both the hotter climate and the more xerophyllous vegetation—combined probably with the poorer peasant types of agriculture—have favoured the ass in preference to the horse. This type of climate and environment appears to be equally favourable to the *goat*, whose distribution almost exactly parallels that of the ass.

The most widely and uniformly distributed livestock shown in Table 5.1 are, however, the *cattle* and the *sheep*. There are, of course, individual differences in distribution, notably the higher proportions of sheep in the predominantly pastoral continents of Africa and Australasia and of cattle in the more densely populated continents of Europe, North America and Asia, where agricultural settlement not only demands draught oxen for the cultivations (and dairy stock for milk) but furnishes both grain and straw for cattle fodder. But by and large both sheep and cattle are evenly distributed throughout each continent and, indeed, throughout each major region of each continent.

Such distribution does not, however, indicate phenomenal adaptations within a single type, as might be interpreted from the table; rather, as will be shown later, it stems from the existence within these two classes of stock of a wide variety of diverse types, each climatically suited to its own particular environment.

Finally, examination of Table 5.1 indicates a marked parallelism in distribution between the *poultry* and the *pigs*. It is, of course, true that both tend to draw their sustenance from identical sources, *i.e.* from the scavenging of the village and the countryside. The distribution of the pig is, however, markedly affected by the religious sentiment against the consumption of its meat, a factor which applies particularly to Northern Africa and Western Asia. In Far Eastern and parts of Southern Asia consumption (notably by the Chinese) is, however, high, and this counterbalances what would otherwise be a lower continental figure. To generalize about the distribution of the pig is difficult. On the one hand it is claimed to have no marked heat tolerance (ROBINSON and LEE, 1941); on the other its distribution is so widespread that it would seem as if some special factor must be operating to enable it to tolerate extremes of climate. Existing knowledge in this field is still so fragmentary that it would be premature to dogmatize. The distribution of poultry is dealt with in Chapter 7.

GENERAL PRINCIPLES GOVERNING FORM AND FUNCTION IN DOMESTICATED ANIMALS

It is clear from the foregoing discussion that climate must be accepted as the most important single factor which influences the distribution of domesticated animals, in particular the environmental temperature and the rainfall. Before describing in detail the characteristics of the individual classes of domesticated livestock, it will, however, be desirable to indicate certain broad principles which are known to affect the relationship between form and function on the one hand and both the direct and indirect effects of climate and of certain other environmental factors on the other. The formulation of these principles has been based largely on observations made by the earlier zoologists on non-domesticated species but, as will be shown later, they are no less applicable to domesticated stock.

DIRECT CLIMATIC EFFECTS

Size and Conformation

It would be out of place in this chapter to discuss in detail the relation of heat production and heat loss to the weight, linear measurements and surface area of the animal body. A very full description of the subject is available in BRODY's (1945) monumental monograph. It will be sufficient to state that under identical conditions the losses of heat by warm-blooded animals may be assumed to be roughly proportional to their surface areas. But in animals of comparable conformation the larger (and therefore the heavier) the body the smaller will be the proportionate surface area, since volume (and therefore weight) increases as the cube of the linear dimensions and surface area only as their square. Hence it might be anticipated that in a cold environment a large body, with a relatively smaller surface area and therefore a reduced heat loss, would be of advantage, while in a hot environment a small body with a relatively larger surface area for heat dissipation would be advantageous. BERGMANN (1847) appears to have been the first observer to have applied this principle to the relation between environmental temperature (and therefore latitude) and the distribution of animals. In broad terms his generalization (usually known as *Bergmann's Rule*) implies that warm-blooded species in the colder northern climates tend to be larger in size than do comparable species in the warmer southern (i.e. tropical) regions*.

The constancy of the relation between size and surface area will, however, clearly only hold true for animals of comparable conformation; any marked deviation in shape, and particularly in the size and proportions of the peripherae, will modify the relationship. ALLEN (1877), in studying the influence of physical conditions on the genesis of species, observed marked differences in the relative sizes of the peripherae of the same species under different climatic environments, and concluded that there was a general tendency for the enlargement of the peripheral parts under conditions of high temperature or towards the tropics (*Allen's Rule*). This generalization is, in fact, an amplification of Bergmann's Rule, since an increase in the size of the peripherae will result in a substantial increase in surface area and therefore in the potentialities for heat dissipation. Conversely in a cold climate a reduction in the extremities, resulting in a more compact body conformation, will decrease the surface area and therefore the heat loss. Allen's own studies were concerned chiefly with smaller mammals, and he noted particularly the variations in the size of the ears, the conformation of the neck and the length of the legs and tail. His only comment on domesticated species was a reference to the length of the bovine horns, which he assumed to increase from the colder to the warmer latitudes. Although the validity of this particular conclusion is open to doubt, the more general application of his rule to the conformation of domesticated livestock is without question of very real significance. Moreover although in domesticated animals such an apparently minor characteristic as size of ears might be assumed to be of little consequence, from the ecological aspect it may in fact constitute a valuable index of the effect of the purely *natural* environment, since it will be independent of any process of selection based on specific human requirements, *i.e.* on selection for draught, milk, meat or wool.

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* The terms 'northern' and 'southern' have been used throughout this chapter for convenience, though they strictly apply, of course, only to the Northern Hemisphere. The same general principles are applicable *mutatis mutandis* to the Southern Hemisphere, though the terms must then be reversed.

It is perhaps relevant to note that the importance of surface area in relation to heat conservation and heat loss will be largely independent of the actual cooling mechanism—whether this is due to conduction, convection or radiation or to evaporative cooling, either from insensible perspiration or sweating. A more detailed discussion of this aspect of the subject will, however, be found in Chapter 6.

The Body Covering

The nature and extent of the body covering, which is in actual physical contact with the external environment, will clearly be a factor of major importance in determining animal adaptation and distribution. It may be most conveniently considered in relation to three properties—the nature of the external coat, the thickness of the skin tissues, and the pigmentation of both skin and coat.

Nature of the External Coat.—As early as 1854 WILSON, in a description of the coats of mammals, distinguished between what he termed the bristly external hair and the soft woolly fibres which are commonly hidden beneath these coarser hairs. He instanced the sheep as an exception to this observation on account of the abundance and length of the woolly fibres and the almost total disappearance of the coarser coating, and he stressed the fact that in cold countries animals tended towards the fleecy coat of the sheep, whereas in warm regions hair was more strongly developed and wool almost totally absent. The proportional abundance of the latter he held to be in inverse ratio to the temperature, while the former was directly proportional to it. This description, while it could be amplified as a result of more recent studies by DUERDEN (1927), BONSMA (1943) and others (see BARKER, 1931), could hardly be improved upon as a broad generalization, and might well merit (with Bergmann's and Allen's Rules) the convenient designation of *Wilson's Rule.*

Such a simplified conception does not, of course, take account of the varied distribution of the coat covering over the body surface, or of the changes in its nature from birth to maturity, or of the seasonal changes in the length of hair and wool (and of their shedding) which take place in most mammals, and which are dealt with in a subsequent chapter. From the wider ecological aspect, however, and particularly from the point of view of animal distribution, such variations are of minor importance in comparison with the general nature of the normal coat covering which is so admirably defined in Wilson's Rule. But it should be noted that while this rule is based primarily on purely temperature considerations, the coat covering may also be designed to protect the animal from other adverse climate factors, notably cold rains and (in animals subject to excessively cold environments such as the reindeer) the penetrating effect of blizzards. It is for this reason that arctic livestock, in spite of their geographical location in the extreme northern latitudes and contrary therefore to Wilson's Rule, frequently possess in place of a woolly coating an ample bristly *hair* pelage which even the strongest winds cannot blow apart (HESSE *et al*, 1937).

Thickness of the Skin.—Earlier observers appear to have paid little attention to the thickness of the skin as a protection against unfavourable climatic conditions; selection for thick skin appears, indeed, to have been associated largely with immunity from attack by insects, and particularly by tick-disease vectors, or with protection from xerophyllous thorny vegetation. Contrary to expectation (since a thick skin might be considered of value as an insulating medium against cold) the only detailed study of skin thickness in relation to climate which appears to have been published indicates that its value is more likely to reside in its protective effect from the direct heat of intense insolation (BONSMA, 1940). Evidence on the subject is, however, scanty, and further research is clearly called for.

Pigmentation of Skin and Coat Covering.—The factors governing the pigmentation of human skin are complex (FLEURE, 1945) but there is in general a rough gradient from the poles to the equator, the skin being white or near-white in the northern races, brown in the sub-tropical belt, and black or near-black in the equatorial regions. The reasons for these differences are still not clear, particularly as it might be anticipated—if pigmentation is related to protection from intense insolation (especially in the ultra-violet)—that in the hotter areas a white reflective surface would be preferable to a black absorptive one (BRODY, 1948). Such differences in human skin pigmentation are, however, paralleled in animals and led GLOGER, as early as 1833, to enumerate the principle that animals inhabiting warm and humid regions show greater melanin pigmentation than the same species in cooler and drier regions, and that in arid desert regions the skin is characterized by the accumulation of yellow and reddish-brown phaeomelanin pigmentation (*Gloger's Rule*). It will be noted that Gloger attributes black pigmentation not merely to temperature (rather than to insolation) but to the combination of temperature and humidity. It will be seen later that his conclusions are at least partially supported by evidence from the pigmentation of certain classes of domesticated livestock.

Gloger's observations and conclusions referred, however, not only to actual skin pigmentation, but to the general pigmentation of the body covering, *i.e.* including feathers and fur. His conclusions were subsequently supported by Allen (1877) who re-emphasized the association with humidity and aridity, but who pointed out that, while animals showed striking instances of geographical variation in colour, they tended at different latitudes to vary in intensity of tints rather than in actual colour—as instanced, for example, in red squirrels and foxes by the gradient from yellowish in the north to deep reddish in the south.

It is perhaps unfortunate for the development of the general subject of animal pigmentation and coloration that most current studies have been concerned rather with colour as a protection against animal predators, with animal mimicry and with the functions of animal coloration in relation to courtship and mating, rather than with the wider ecological aspects of its relation to climate (PEARSE, 1939). A reorientation of interest in this direction would be of real value from the aspect of the ecology of domesticated livestock.

INDIRECT CLIMATIC EFFECTS

Without question the most important *indirect* effects of climate on animal distribution are those due to the influence of rainfall on the nature, quality and seasonal growth of vegetation. This affects not only the size and conformation, as well as the density, of the animal population but their grazing habits and range (and hence their means of locomotion) and the structural formation of their digestive tracts. A second indirect effect of climate is its influence, in conjunction with the local geological structure of the land surface, on the nature of the terrain and hence on the development of specialized structural adaptations which enable an animal to cope with its physical environment. All these must be taken into account in any attempt to relate climate to animal form and distribution.

Size and Conformation

Reference has already been made to the interrelationship between environmental temperature and body size. An animal can, however, only achieve its optimal body size if its surroundings furnish a constant and adequate supply of good quality fodder for which a satisfactory combination of temperature and rainfall are essential. The ideal conditions for grazing are a temperate climate and well spaced rainfall, a combination found ideally in, for instance, New Zealand. Such conditions permit all-the-year-round grazing on a herbage which grows at such a rate and on such a soil medium as to furnish a well balanced source of nutrients. It might be assumed that similar optimal conditions would be furnished in the wet tropical areas, where a high environmental temperature is balanced by a correspondingly high rainfall. Although the evidence on this point is conflicting, there is nevertheless a widespread impression that the excessive rate of plant growth in such areas leads to the production of a lush vegetation of inferior nutritive value. Moreover the leaching effect of constant high rainfall is apt to result in mineral deficiencies in the soil, which may in turn be reflected in the composition of the vegetation. In seeking for an explanation of the dwarfing of animals which is universally found in the hot-wet tropics (and which is often paralleled in animals grazing on leached hillsides in the cold-wet temperate areas) this indirect climatic effect cannot be ignored.

But it is in the semi-arid and desert areas of the world that the indirect effects of the climate are most obvious, both in regard to the size and the conformation of the animal population. In regard to size, the extreme seasonal variations in rainfall, which are inevitably accompanied by an extreme seasonality in plant growth, results in one of two alternatives; either the animal has to face periods of serious food scarcity, during which not only will growth cease but substantial weight losses may be suffered (a subject on which there is very little reliable quantitative data (BONSMA *et al*, 1953)); or it is necessary for it to migrate for long distances in search of food, in which case a considerable proportion of the assimilated nutrients are rendered unavailable for growth. In either event the result is apt to be either a markedly retarded development towards maturity, or a modification in body structure, or permanent stunting.

It is as a safeguard against the more extreme risks of the desert areas (where the rainless and therefore the vegetationless period may extend to four or five months or more) that the metabolism and conformation of certain animals has been so modified as to permit the accumulation of a substantial localized fat reserve in the body. In regard to conformation this is, of course, best seen in the development of the hump in Arabian and Bactrian camels, but it is of no less importance in the fat-tailed and fat-rumped sheep of Africa and Asia and indeed in man himself, *e.g.* in the steatopygia of the Hottentot of Southern Africa.

The localization of a large fat reserve in a single organ may incidentally confer some small advantage on animals in hot climates, since in consequence they do not need a generalized subcutaneous layer (such as that present in temperate livestock) which forms an insulating layer capable of preventing the dissipation of body heat. The fact that localized fat reserves are not commonly found in animals other than those which normally inhabit desert and semi-arid areas clearly indicates, however, that these are *primarily* associated with the provision of stored energy rather than with the non-insulating properties of the body covering. The distribution of fat in animals inhabiting cold desert areas (*e.g.* the Bactrian camel and the yak) would in this connexion form an interesting study.

Other Natural Adaptations

The effect of climate on soil and vegetation has resulted in certain additional structural adaptations to which brief reference should be made, since they affect both the conformation and habits of the livestock concerned. The first and most obvious are those related to locomotion.

It has already been noted that in desert areas animals may need to cover long distances in search of food owing to the extreme seasonality of the rainfall. It is not surprising therefore to find that most desert animals are exceptionally long-legged. This applies not only to cattle, sheep and camels but to the equines which inhabit the northern deserts (*e.g.* the ponies of the Gobi Desert) and to the asses which border on the more southern African deserts. Allied to such adaptations are those connected with the nature of the terrain. Typical examples are the reindeer's hoof which facilitates travel over deep snow, the large flat foot of the camel which has to move over shifting sand, and the mechanisms controlling the sure-footedness of the mountain goat and sheep which permit grazing on steep and rocky hillsides. An adaptation of a rather different nature is the razor-back conformation of the pig in jungle areas, which enables the animal to penetrate dense vegetation in search of food.

The second type of specialized adaptation is that associated with the nature of the vegetation from which the animal derives its sustenance. Thus, while the sheep's teeth and mouth structure are well known to be adapted to the grazing of close growing herbage, those of the goat are adapted to browsing on low bushes, shrubs and herbs typical of the vegetation in semi-arid areas—a feature which incidentally renders the goat much less prone to intestinal infestation (LOWE, 1943). The most striking adaptation of this nature is, perhaps, that of the camel and other species which derive their nutrients from highly xerophyllous vegetation. Although the upper lip is sufficiently sensitive to enable such animals to pick up loose leaves or grains from the ground, the tissues round their mouths appear to be impervious to injury by the thorny vegetation typified, for instance, in various species of acacia, which abound in their natural grazing grounds (LEESE, 1927).

Associated both with the nature and the quantity of the vegetation, though only indirectly affecting external conformation, is the structure of the digestive tract which, in herbivores (and particularly in ruminants) occupies an exceptionally large proportion of the body cavity and which therefore necessitates a barrel of correspondingly large capacity. Both in this respect, and in regard to the more general factors which influence conformation, a systematic study of the comparative morphology of the world's domesticated livestock would be of very great value in elucidating the underlying causes of existing animal form and distribution.

ADAPTATIONS TO MEET HUMAN NEEDS

Any general discussion of the factors affecting the structural adaptations of domesticated animals would be incomplete without at least a brief reference to the changes brought about by their symbiotic association with man. This association has modified the environment of livestock in three main directions—in their localized climatic surroundings, in their sources of food, and in the degree of their specialized functional development.

Where animals are capable of intensive domestication, their localized climatic surroundings may be entirely altered by the adoption of all-the-year-round housing. Since this involves large capital expenditure and large labour requirements (as well as large quantities of conserved and transported food) it is usually only possible with the smaller livestock and particularly with those which are quick maturing and capable of a high level of productivity. All-the-year-round housing has therefore in general only been applied to poultry and, in a modified form, to pigs. The more usual practice with the larger classes of livestock is to furnish housing or shelter only for the climatically less favourable periods. Examples are the almost universal practice of housing cattle throughout the winter period in the colder latitudes and of providing shelter from the sun in hotter areas. Such seasonality in housing is adopted not only because protection is unnecessary in the less harsh months but because, since natural grazing furnishes by far the cheapest form of food available to livestock, it provides the only economic means of livestock rearing. From the practical aspect it is important to note that the modification of a cold environment by housing is far easier and cheaper than the modification of a hot environment, which can (except with the most primitive types of shelter) only be achieved by expensively constructed and air-conditioned buildings. From this aspect animal adaptations which furnish a high heat tolerance are far more valuable than those associated with tolerance to cold.

As regards the provision of food, the outstanding advantage to the animal of association with man is the possibility of the more regular supply of fodder which can be achieved either by the conservation of the naturally occurring herbage or, in agriculturally settled areas, by the provision of the by-products of human crop production and the growing of specialized animal feeds. The latter are, from the point of view of meeting the human need for animal products, of special value, since they furnish nutrients in a concentrated form which is essential to rapid animal growth and high productivity. On the other hand the aggregation of animal populations which becomes possible with artificial feeding and housing involves new risks of disease and parasitic infestation which—if not countered—may result, if not in excessive mortality, at least in stunting and lowered productive capacity. Where (as in India) there is added a religious sentiment against the slaughter of the old or surplus stock, the results on growth and size and productivity may be disastrous.

Such dangers are largely avoided in desert and semi-arid areas, where seasonal migrations are as essential for herds of domesticated livestock as for the naturally nomadic animal populations, not only for grazing vegetation but for water. In these areas, however, there still remains, somewhat surprisingly, the danger of over-population, partly through the desire of herd owners to maintain the maximum animal population on what are in essence free grazing lands, and partly through excessive competition for access to the limited water points. Moreover, although parasitic infestation is largely avoided in nomadic grazing, the extensive movements of stock conduce to the spread of contagious diseases which—over such vast areas—are difficult either to control or to treat. On balance the advantages of the more intensive type of husbandry, with its more ample and constant supplies of food and its provision of shelter from the extremes of climate, undoubtedly outweigh those of the more extensive nomadic grazing, though each have their place in nature and each have their inherent dangers.

It is, however, predominantly under artificial conditions of feeding, housing and management that the specialized functional developments which are of particular value to man have been developed. These have affected not only the overall body size (since optimal and uninterrupted growth is possible over the whole life span) but no less its external conformation. Thus may be instanced the square and compact body of the meat-producing breeds of both cattle and sheep, the length of leg and general conformation of the working bullock and the horse, the heavy body covering of hair or wool of the Angora goat, the alpaca and the sheep, and the wedge-shaped body and hypertrophied udder of the dairy cow. Such man-made adaptations must clearly be taken into account in assessing the significance of the more natural environmental factors which affect the form, function and distribution of domesticated livestock.

ILLUSTRATIONS OF THESE PRINCIPLES IN EXISTING DOMESTICATED SPECIES

An attempt has been made in the previous section to summarize some of the general principles governing form and function in domesticated animals. In the present section examples will be given of the application of these principles to certain classes of domesticated livestock.

Certain more specialized species which have been mentioned in earlier sections of this chapter, notably the reindeer, the llama and the alpaca, while forming excellent illustrations of adaptation to climate and environment, are scarcely of sufficient general or economic importance to warrant detailed treatment. They have been adequately described by Phillips (1948). Nor are the gayal and banteng sufficiently widespread in their distribution to justify separate consideration. Nor again would it be profitable to include any detailed discussion of the pig which, as already noted, shows for reasons as yet unexplained no very marked climatic gradients either in form or in heat tolerance, while poultry will be dealt with in Chapter 7. The following discussion will therefore be confined to cattle (including buffaloes) sheep, and goats, equines and camels, in this order.

CATTLE

The world's cattle may be broadly classed into seven main types: the yak, which is typical of the cold elevated plateaux of Central and Eastern Asia; temperate (so-called European) cattle inhabiting the cool temperate zones; sub-tropical cattle, of the warm temperate zones; zebu cattle* typical either of the dry plains or of the humid areas of the tropics; so-called Sanga cattle, believed to be derived from the intermingling of long-horned Hamitic and zebu ancestors; and the buffalo which is, as already mentioned, found primarily in the swampy or irrigated areas of the tropics. *Figures 5.3* to *5.12* furnish illustrations of these seven main types. They have been selected to represent, as far as possible, extreme examples of the points which will be dealt with in the course of discussion which, following the broad principles outlined in the previous section, will be confined chiefly to size and conformation, the nature of the body covering, and the importance of certain specialized adaptations.

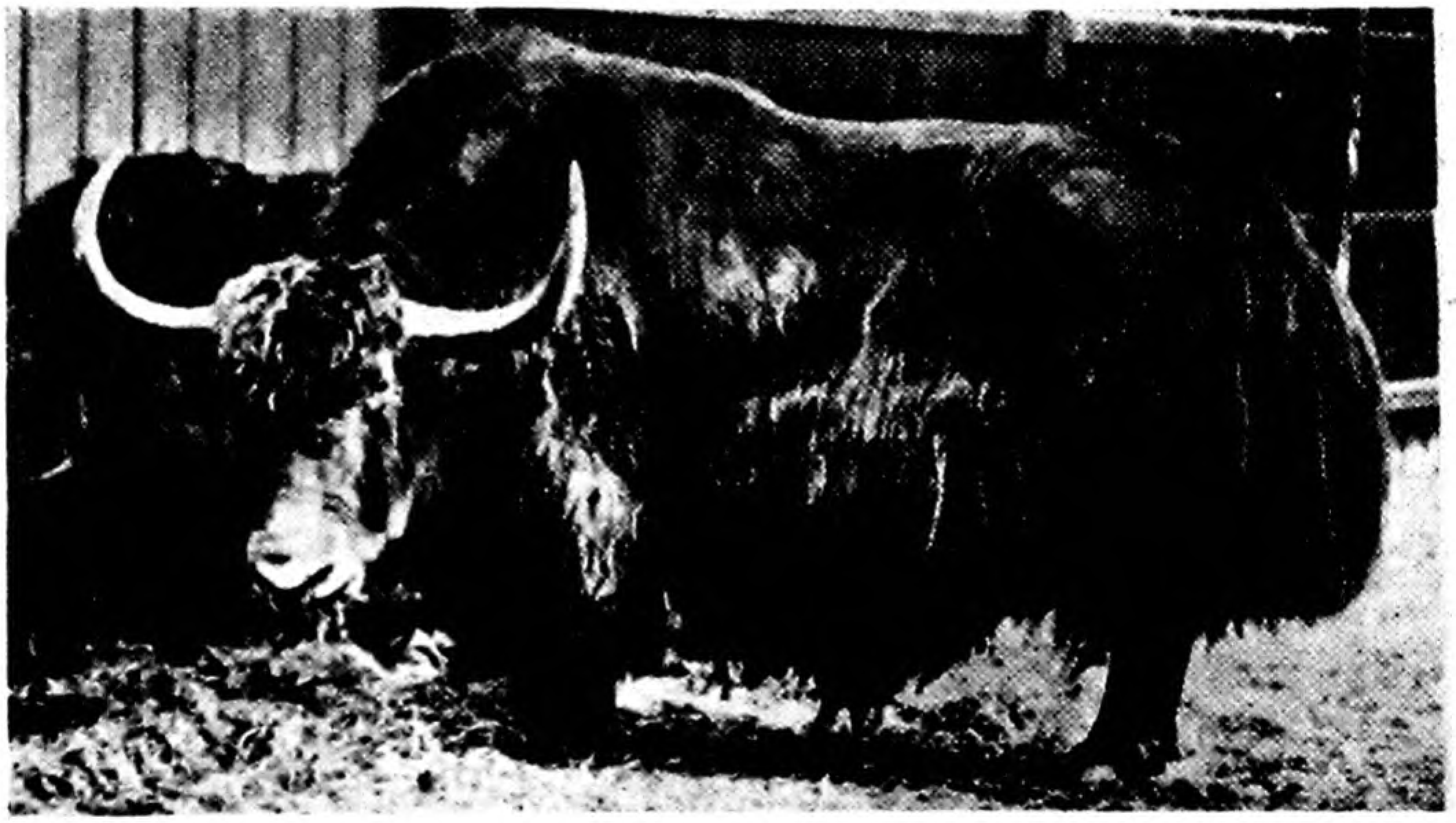

Figure 5.3. The yak (High plateaux of Tibet and Western China). (By courtesy, W. S. Berridge.)

The yak (*Figure 5.3*) possesses a relatively heavy and compact body, with short legs and neck, a relatively small dewlap, a short tail and small ears. It is covered with a copious coat of hair with long fringes around the poll, at the withers and shoulders, along the flanks and on the thighs

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* The lateral horned zebu, or Afrikander, has not been illustrated owing to its very localized distribution.

(PHILLIPS, JOHNSON and MOYER, 1945; PHILLIPS, TOLSTOY and JOHNSON, 1946; WHITE, PHILLIPS and ELTING, 1946). While the true cattle of the cool temperate zones differ markedly in detailed conformation from the yak (as is consistent not only with their ancestry but no less with their long periods of selective breeding for meat or milk), they share with it a tendency to compactness in general body form and, in the more northern breeds, a moderately thick and heavy coat (*Figure 5.4*).

In contrast sub-tropical cattle of the warm temperate zone (*Figure 5.5*), though not invariably smaller in size, have rangier frames with, in general, larger extremities. But from the aspect of conformation their most striking feature is a marked increase in the area of the dewlap, which takes the form of a loose empty fold of skin some 6 to 8 inches in depth and extending from the base of the jaw to the sternum.

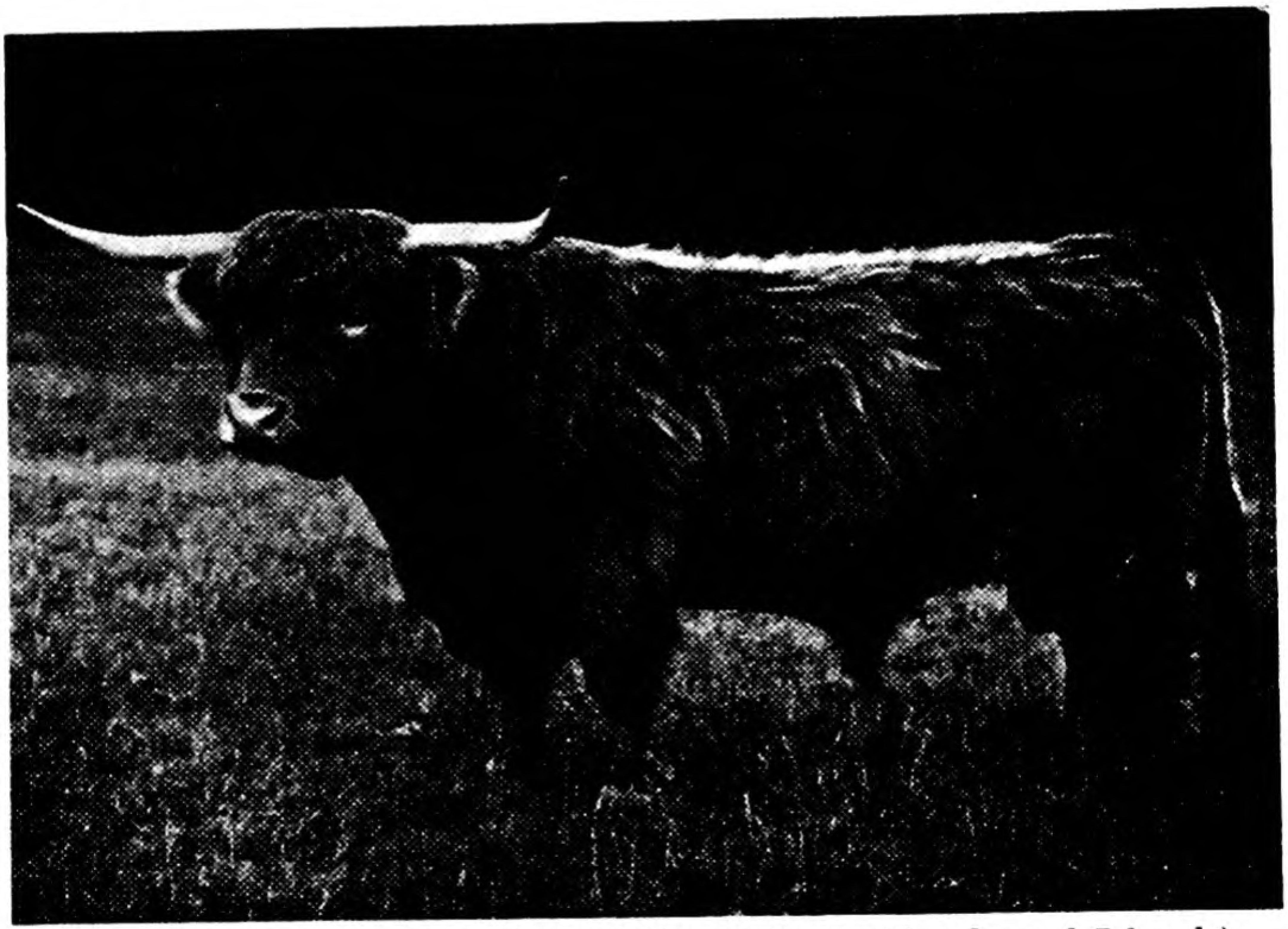

Figure 5.4. West Highland bull (Scottish Highlands and Islands).

This characteristic is exaggerated in the zebu cattle of the dry tropics, whether these have been bred for draught (*Figure 5.6*), or milk (*Figure 5.7*), or meat (*Figure 5.8*). Indeed in the latter the dewlap is not only so loose as to form actual corrugations, but there are continuing folds of skin along the whole of the ventral surface of the body, particularly from the sheath to the scrotum. It may be added that, although the animals in *Figures 5.6* to *5.8* show only moderately enlarged ears, those of certain other breeds of zebu (notably the Gir) are so greatly enlarged and pendulous as almost to meet the end of the muzzle when stretched (WARE, 1939). Moreover, both in the cattle of the warm temperate zone and in the zebu cattle there is a marked

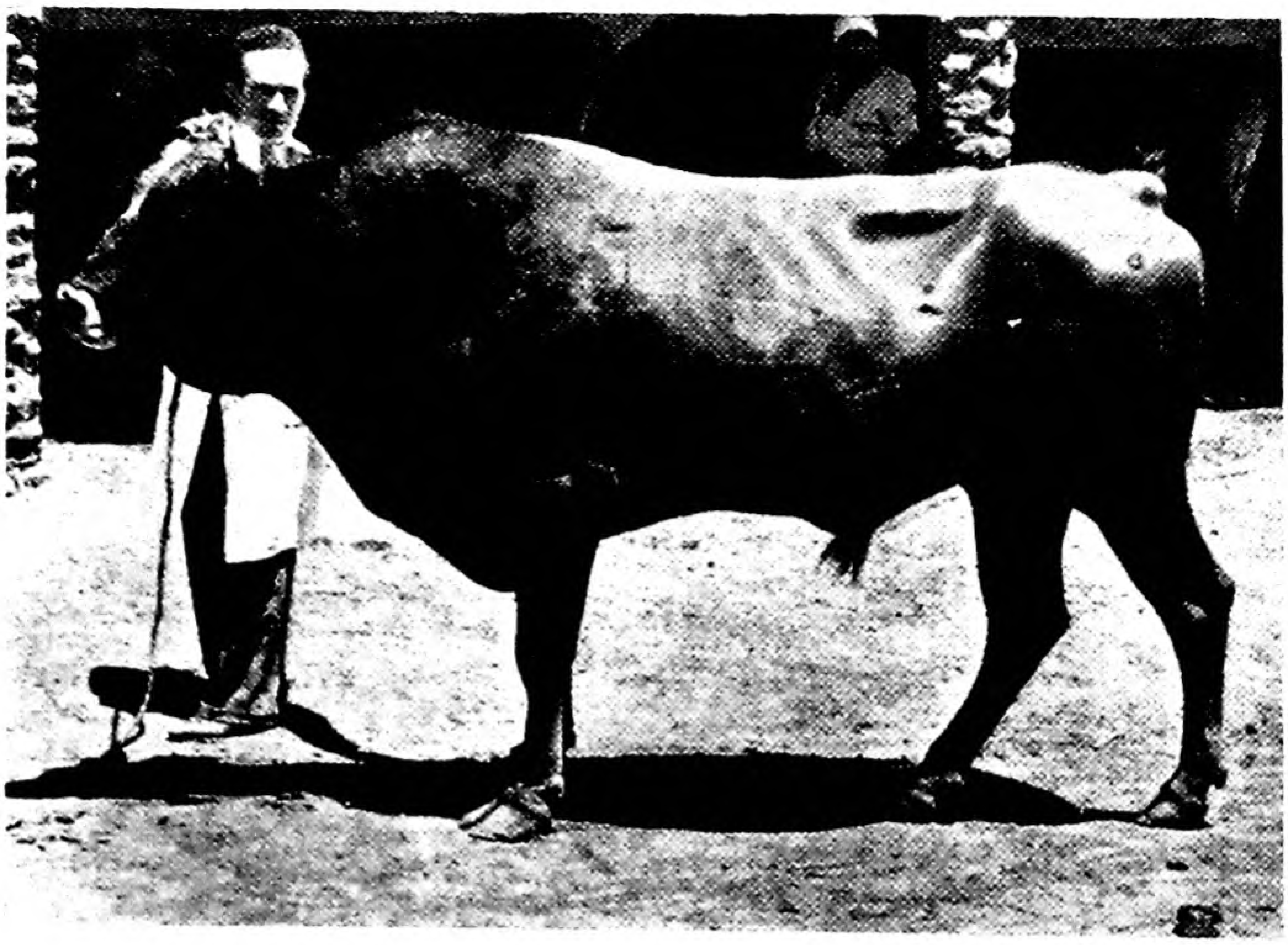

Figure 5.5. Damietta bull (Sirw, Nile Delta, Egypt).

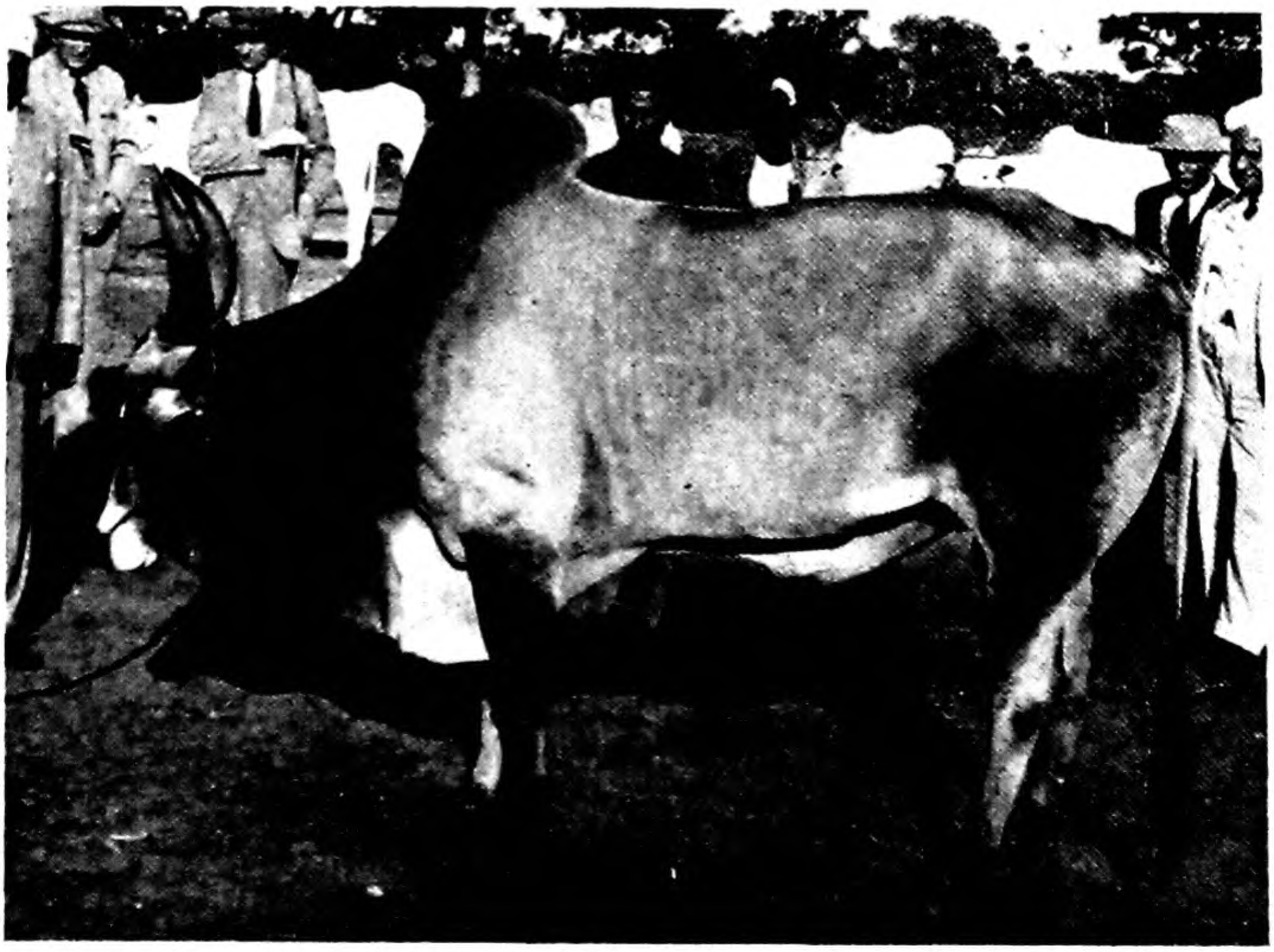

Figure 5.6. Kangayam bull (Palayakottai, Coimbatore, India).

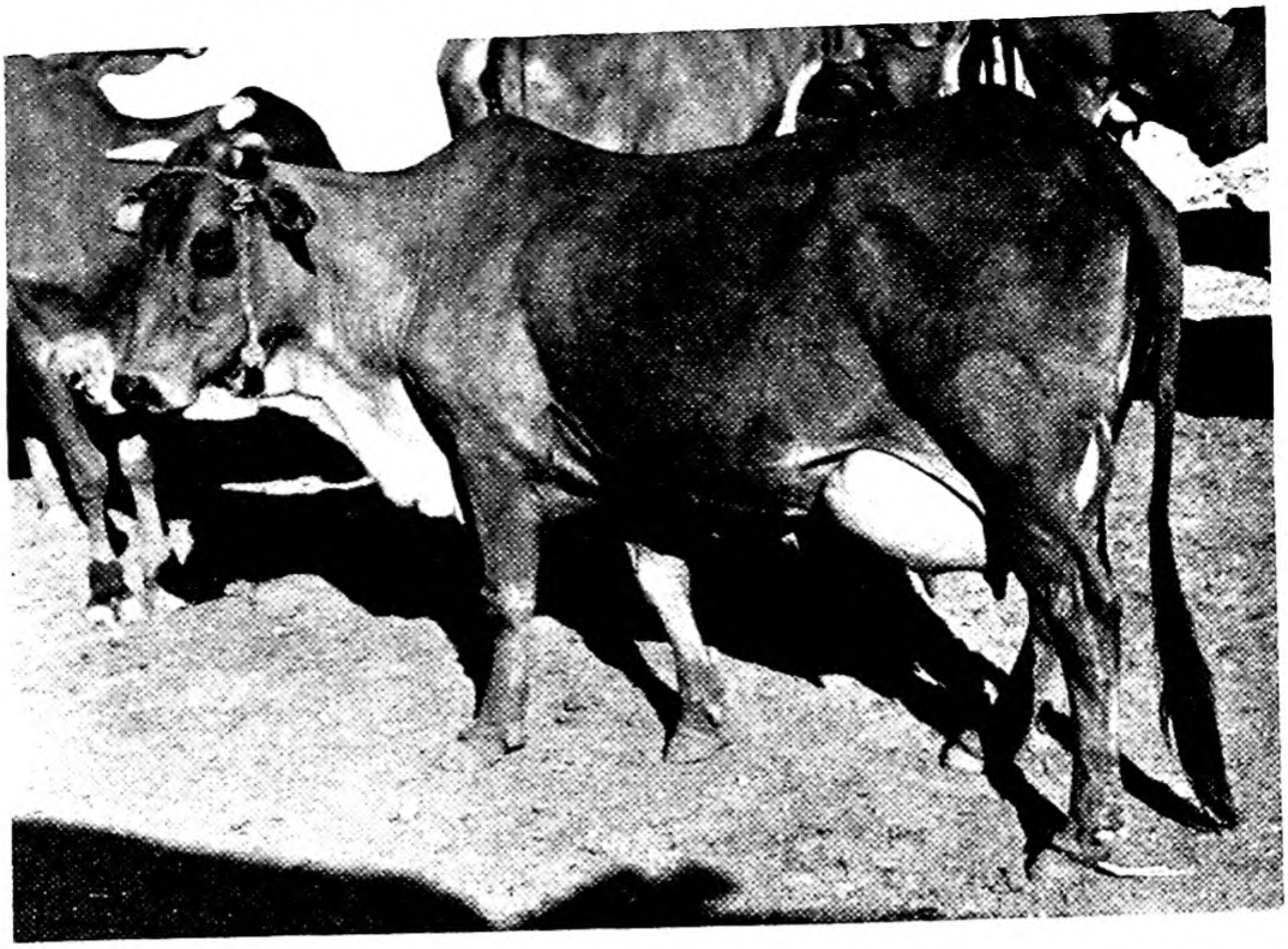

Figure 5.7. Shendi cow (Shendi, Khartoum, Anglo-Egyptian Sudan).

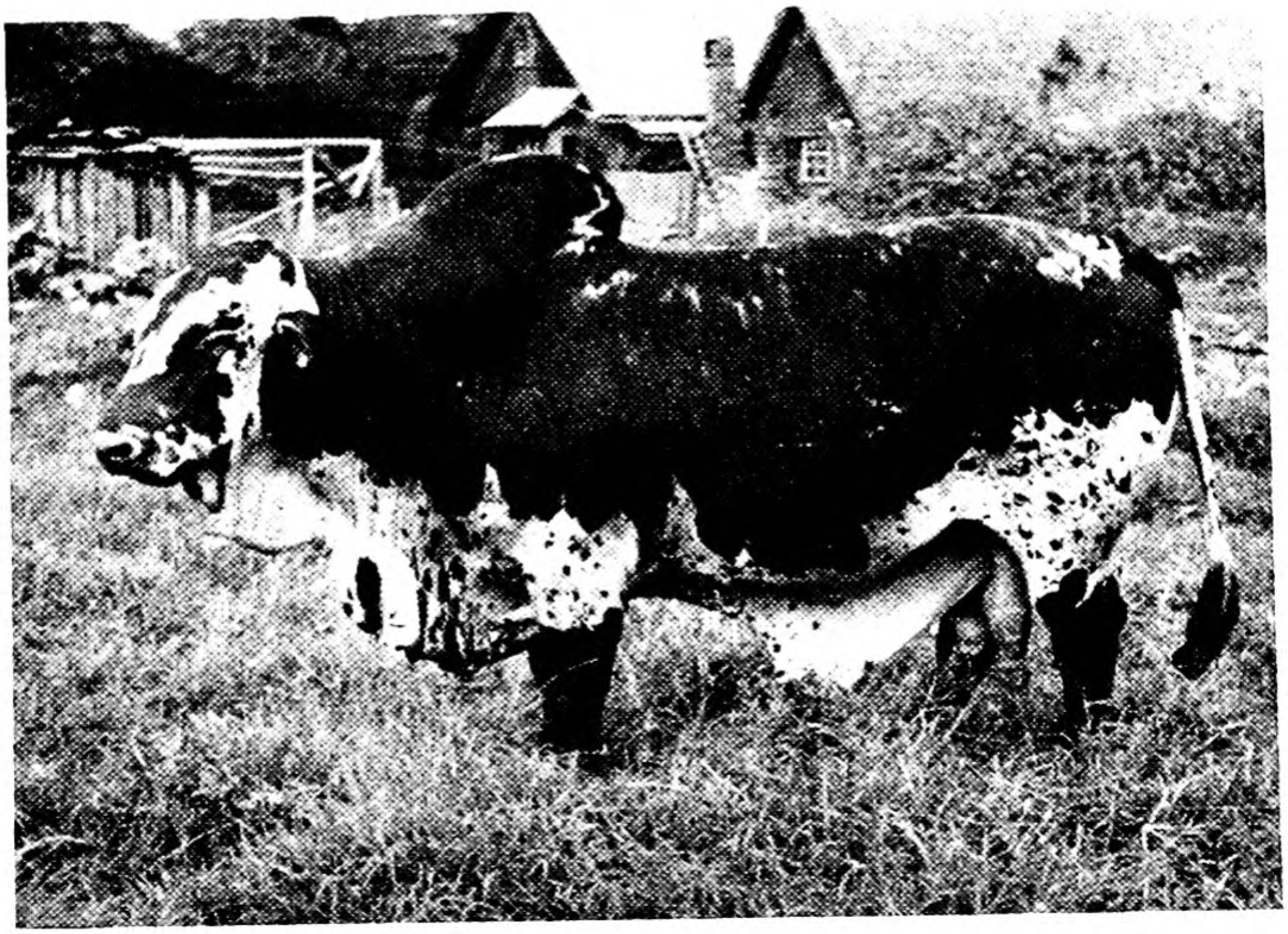

Figure 5.8. Boran bull (Naivasha, Kenya, East Africa).

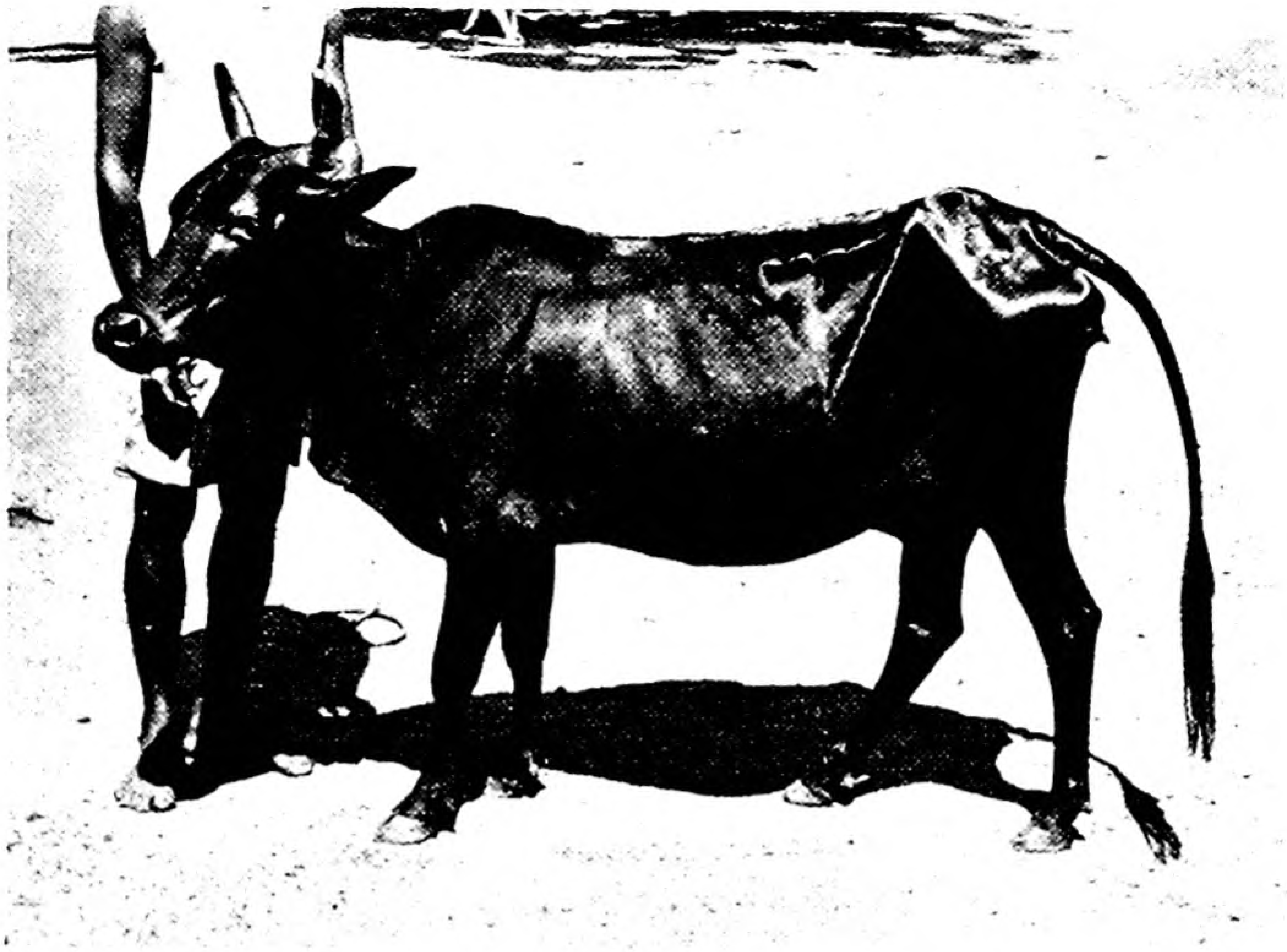

Figure 5.9. Sinhala cow (Labuduwa, Ceylon).

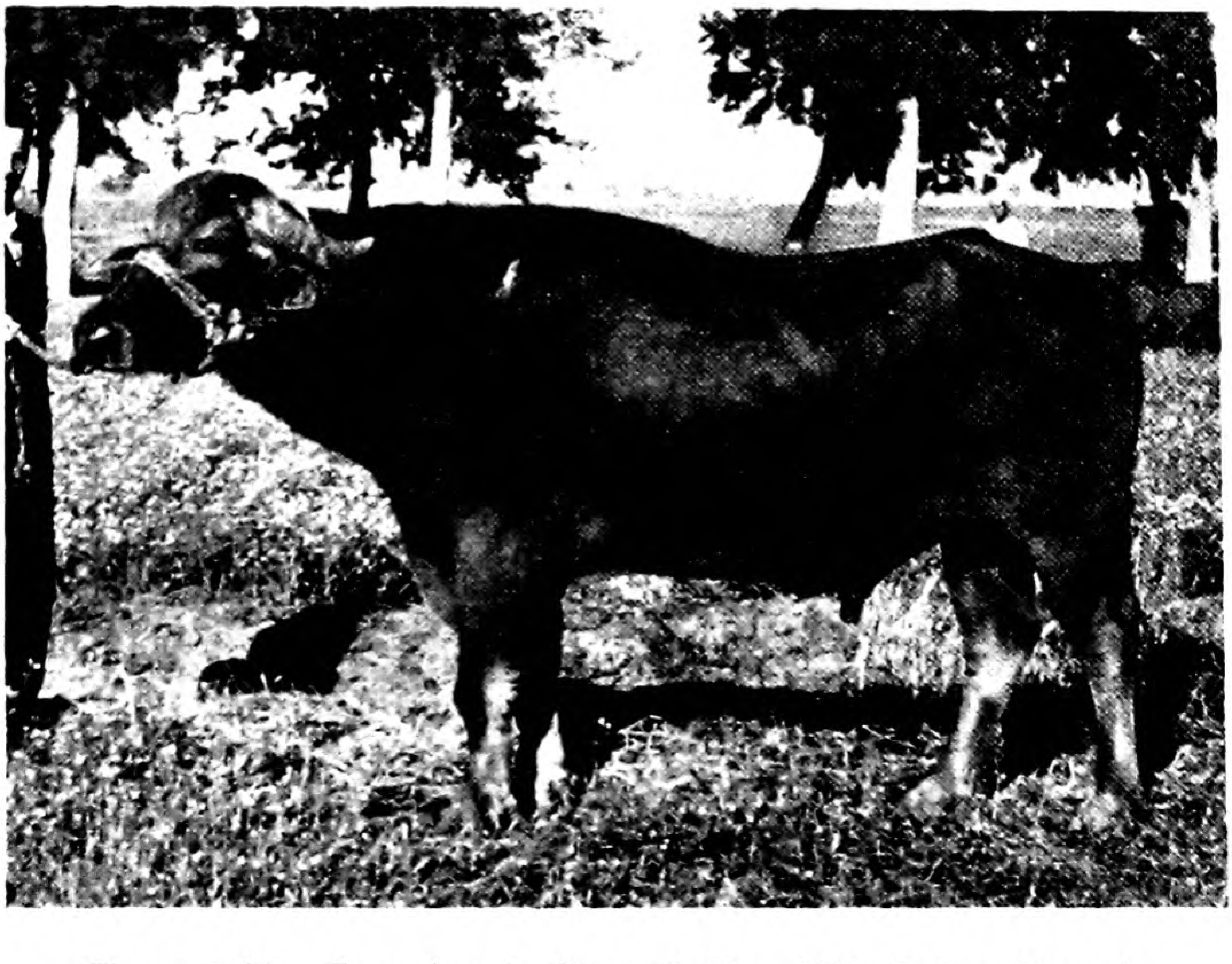

Figure 5.10. Egyptian buffalo (Sakha, Nile Delta, Egypt).

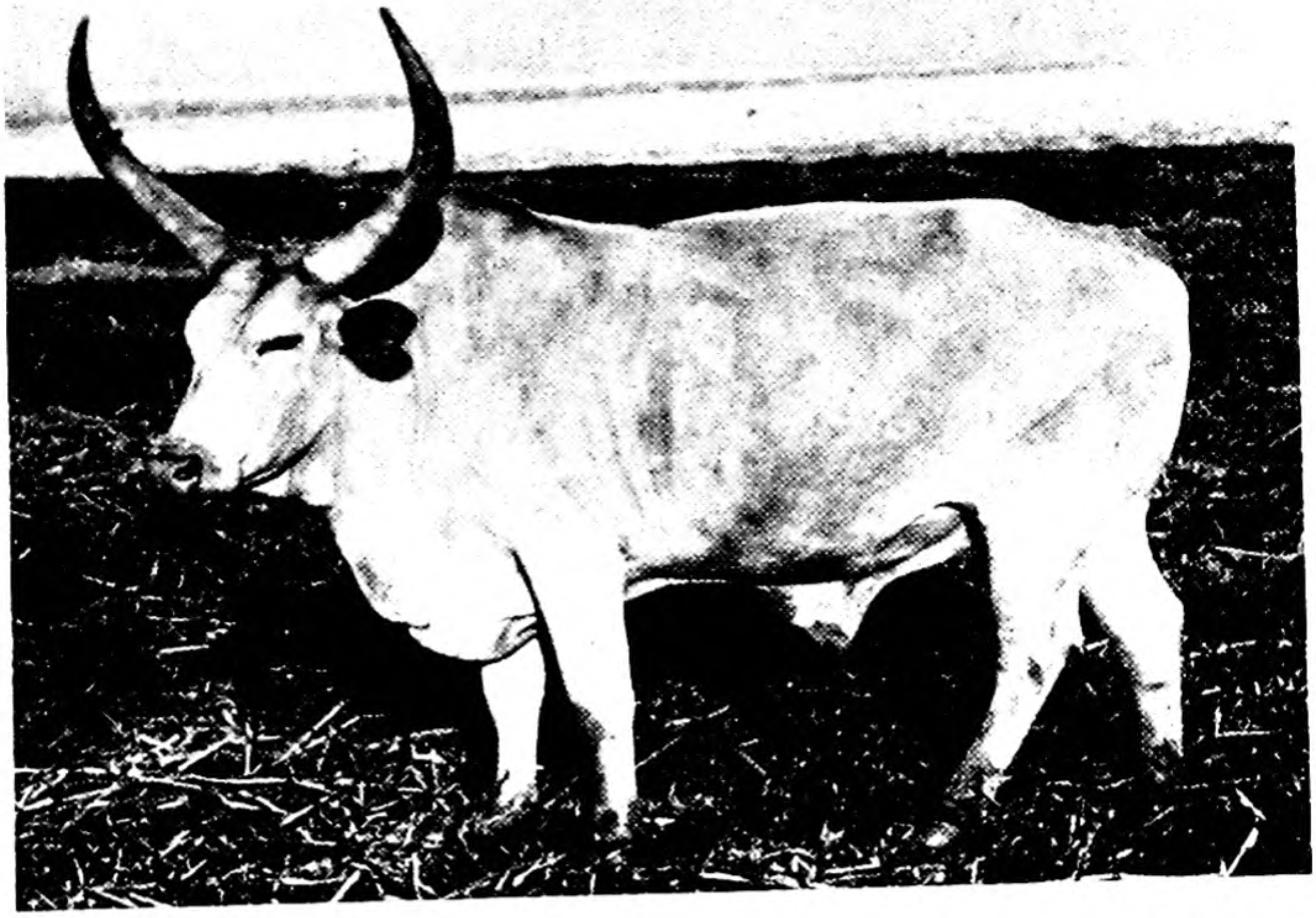

Figure 5.11. Nilotic (Sanga) steer (Malakal, Upper Nile Province, Anglo-Egyptian Sudan).

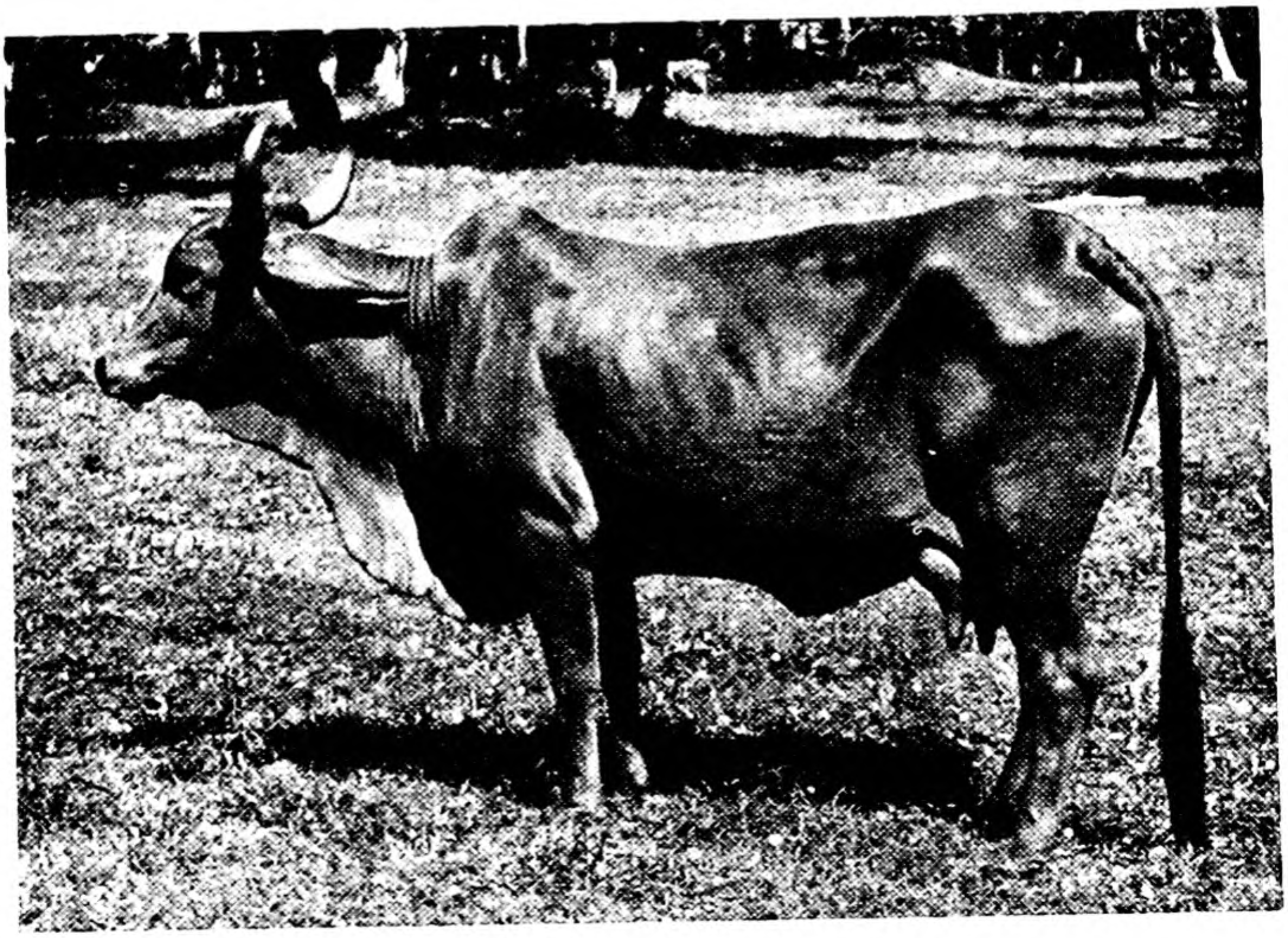

Figure 5.12. Red Sindhi cow (imported from Karachi, India, to Polonnaruwa, Ceylon).

change in the nature of the body covering from the relatively thick dull coat of the more northerly animals to a fine short-haired coat which gives to the surface of the body a characteristic sheen.

So far no mention has been made of size, for because of the widely different origins of domesticated cattle, of the marked local variations in their planes of nutrition, and of the changes in the methods of breeding and management to which they are subjected, it seems *prima facie* unlikely that a close correlation can be expected between climatic environment and stature. Nevertheless, in regard to one type of zebu, *i.e.* those located in the hot-wet areas of the tropics, it does appear that dwarfing is universal (*Figure 5.9*). Similar dwarfing is also commonly found in buffaloes inhabiting the hot-wet tropical regions such as the West Coast of India, Ceylon and the East Indies, though their counterparts in the cooler irrigated areas of, for example, Northern India and the Nile Delta, as well as in the natural marshes of Iraq, attain a much larger stature (*Figure 5.10*). It is also relevant to note that, while the dwarfed zebu possesses the normal fine-haired coat of its larger prototype, both the large and dwarf buffalo have only a very sparse covering of long coarse hairs, but possess, of course, a far thicker skin.

There is one further point of conformation in zebu cattle which is largely responsible for its unique appearance, *i.e.* the hump over the thoracic vertebrae. There seems no doubt that the original purpose of this hump was that of a reserve fat store, and it is still capable of showing (as do the humps of camels) marked seasonal changes in size according to the abundance of the available food supply. On the other hand CURSON and BISSCHOP (1934) have shown that in intermediate types of cattle such as the Sanga (*Figure 5.11*), which are widely distributed over the tropical areas of Africa and which are markedly heat tolerant, the comparable development of a marked thickening in the cervico-thoracic region is of purely muscular origin and bears no relationship to fat storage. Moreover it is also notable that the hump in the female zebu is far smaller and less prominent than in the male (*Figure 5.12*). While therefore the significance of the zebu hump should not be overlooked, particularly to stock located in nomadically grazed areas, its function should be clearly differentiated from those specifically concerned with heat tolerance.

SHEEP AND GOATS

Sheep and goats are not only comparable in size and conformation but exhibit very similar climatic gradients in respect of both these characteristics, as well as in the thickness (though not the nature) of their coats. Moreover their habitats, while not identical, show a marked overlap—as, for example, in the mixed nomadic grazing flocks of the south-western Asiatic deserts. It will therefore be convenient to deal with them together.

The world's sheep may be broadly classed into three main types: the temperate type, typified by a wide variety of breeds extending from northern mountain sheep to the European Longwool and Down breeds (Romney, *Figure 5.13*) and again to southern types like the Merino; the northern desert sheep, typical of the Mediterranean borders of the Sahara and of the desert areas extending through Syria and Iraq into Persia and Kurdestan (*Figure 5.15*) as well as of the more arid areas of China; and the southern desert sheep, found on the southern borders of the Sahara and in the hot plains of Southern India (*Figure 5.17*). The natural distribution of the goat is more limited, being confined to the drier regions of Europe, Africa, and Asia. Its most northerly and coldest natural habitat is in the hilly areas of Asia Minor, the home of the Angora (*Figure 5.14*). A second type is, like the sheep, found in the northern desert areas (*Figure 5.16*), and a third type in the southern desert regions (*Figure 5.18*).

Sheep in the temperate areas (*Figure 5.13*), while showing local variations in size and conformation, are in general of moderate size, compact, with short legs, stocky neck and small ears. They possess thick and compact wool coats. Goats in an equivalently cold environment (*Figure 5.14*) show similar characteristics in body size and conformation; the coat, while consisting entirely of hair (the mohair of commerce) is also correspondingly thick and copious. In size and general conformation both northern desert sheep and goats (*Figures 5.15* and *5.16*) show only slight differences from those of the temperate areas; they tend, however, to be less compact in conformation, with a less stocky neck, longer legs and markedly longer ears. Their coats are still ample, as is indeed necessary to enable them to withstand the cold seasons which are typical of the northern desert climates.* But both wool and hair are coarser and less compact than in the temperate zones. In the hot tropical desert areas both classes of stock exhibit, however, striking changes not only in conformation but coat covering. The southern desert sheep (*Figure 5.17*) show a phenomenal lengthening of the extremities, with long rangy bodies, long legs, elongated necks, and long ears and tails. Moreover the woolly coats are replaced by a covering of fine short hair, comparable in texture to that of zebu cattle. Such hair is generally well distributed over the body, but in certain breeds is largely lacking from the ventral surface. These changes are paralleled in southern desert goats (*Figure 5.18*) which show similar striking increases in the size of the peripherae, notably in the length of legs and ears, and a no less marked change in the nature of the coat which is limited to a covering of fine, short and sparsely distributed hair.

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* It was, for example, reported from one province of Iraq that in 1942 no less than 50 per cent of the ewes died from exposure to cold (BERKELEY, 1943).

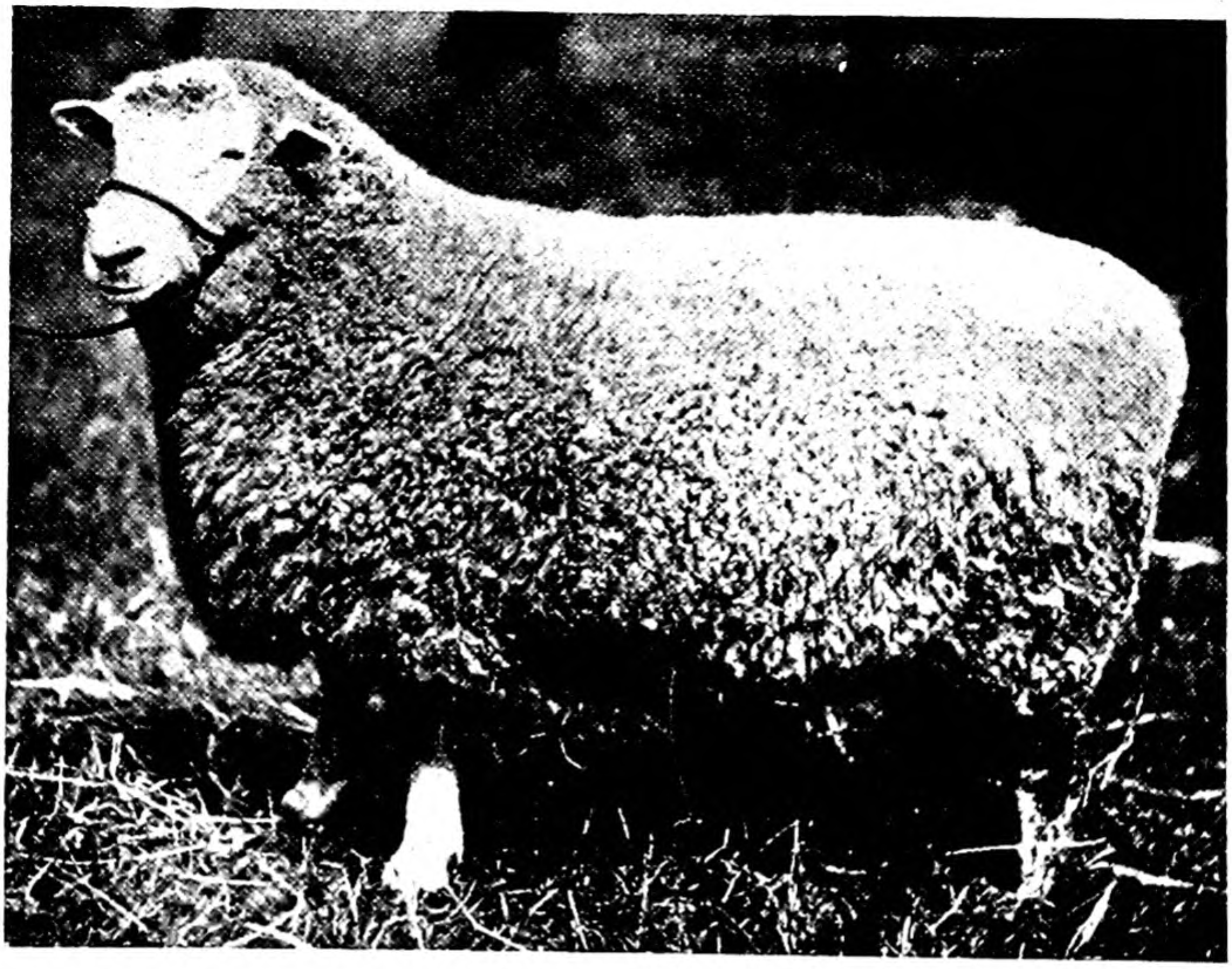


Figure 5.13. Romney Marsh ram (Kent, England).

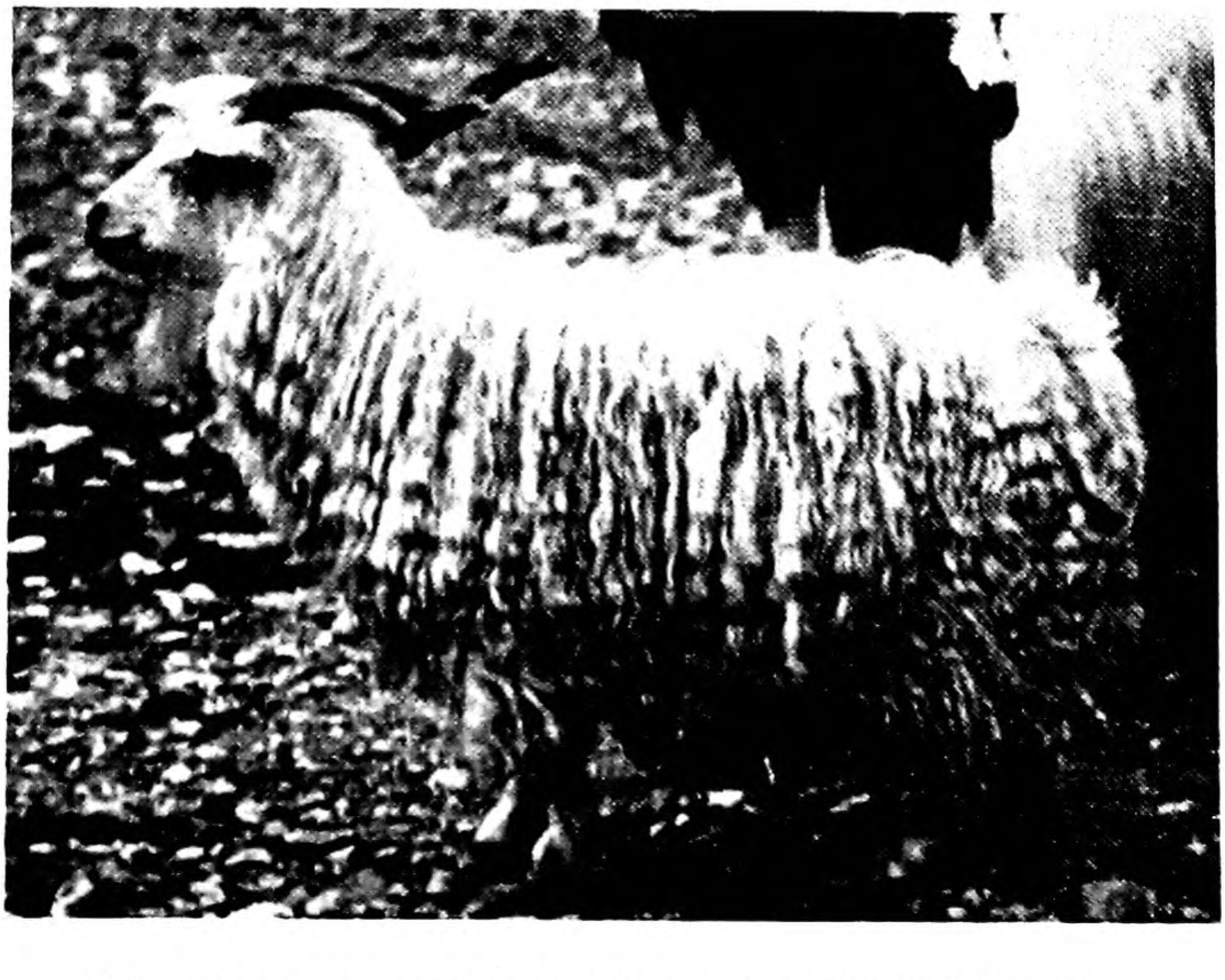


Figure 5.14. Angora goat (Zakho, Iraqi-Turkish border).

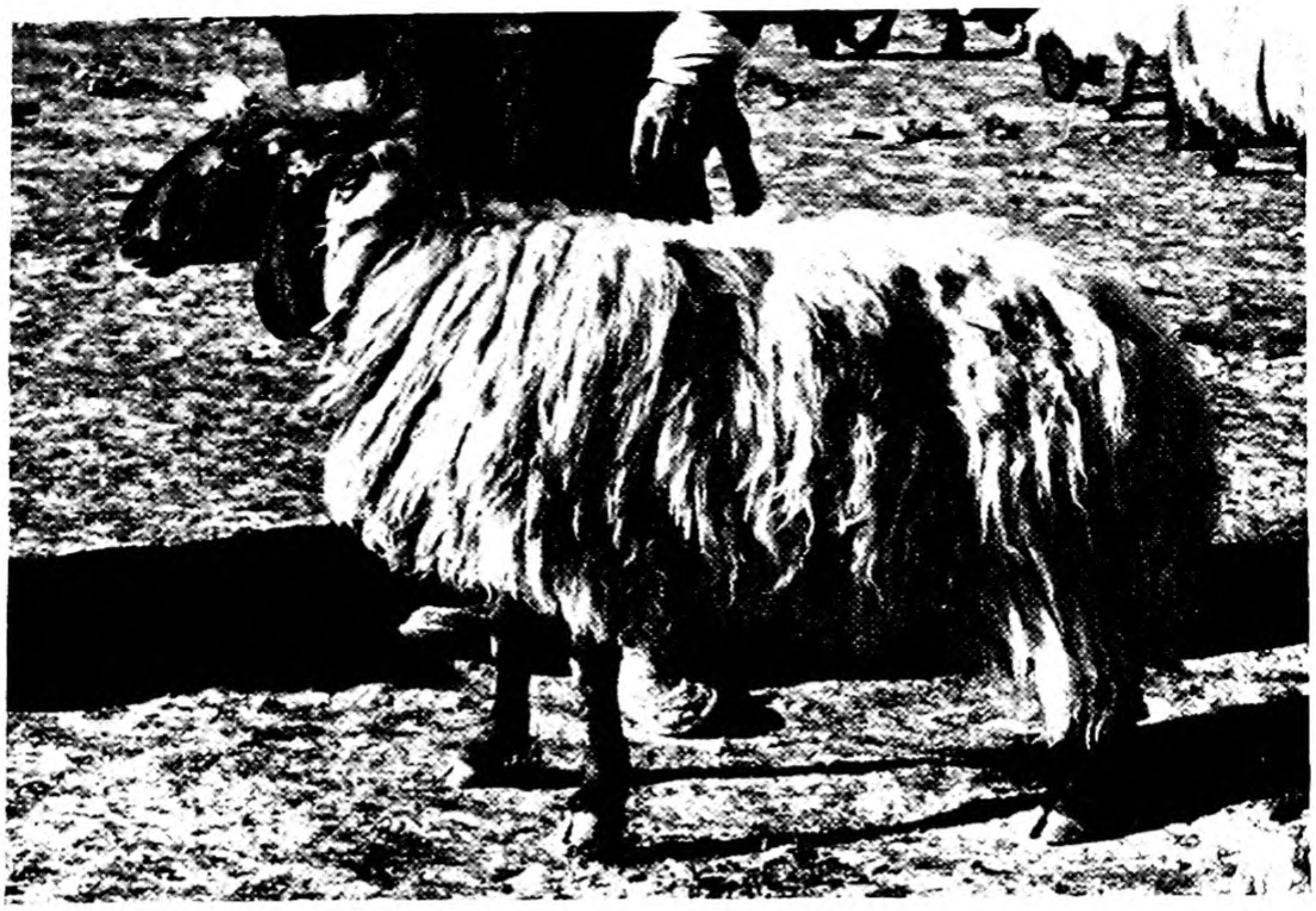


Figure 5.15. Kurdi (Desert) sheep (Erbil, Iraq).

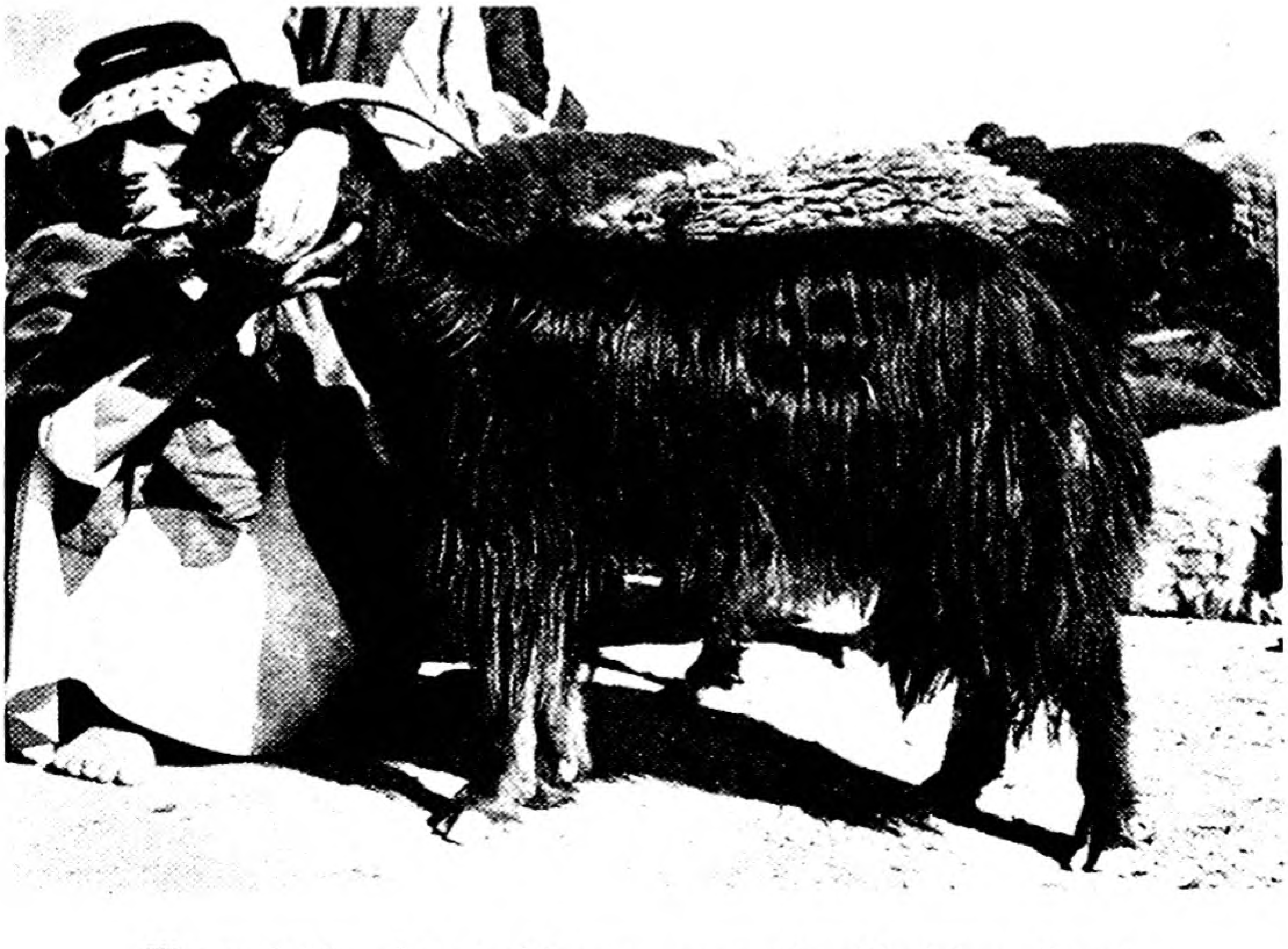


Figure 5.16. Iraqi (Desert) goat (An Nasiriya, Iraq).

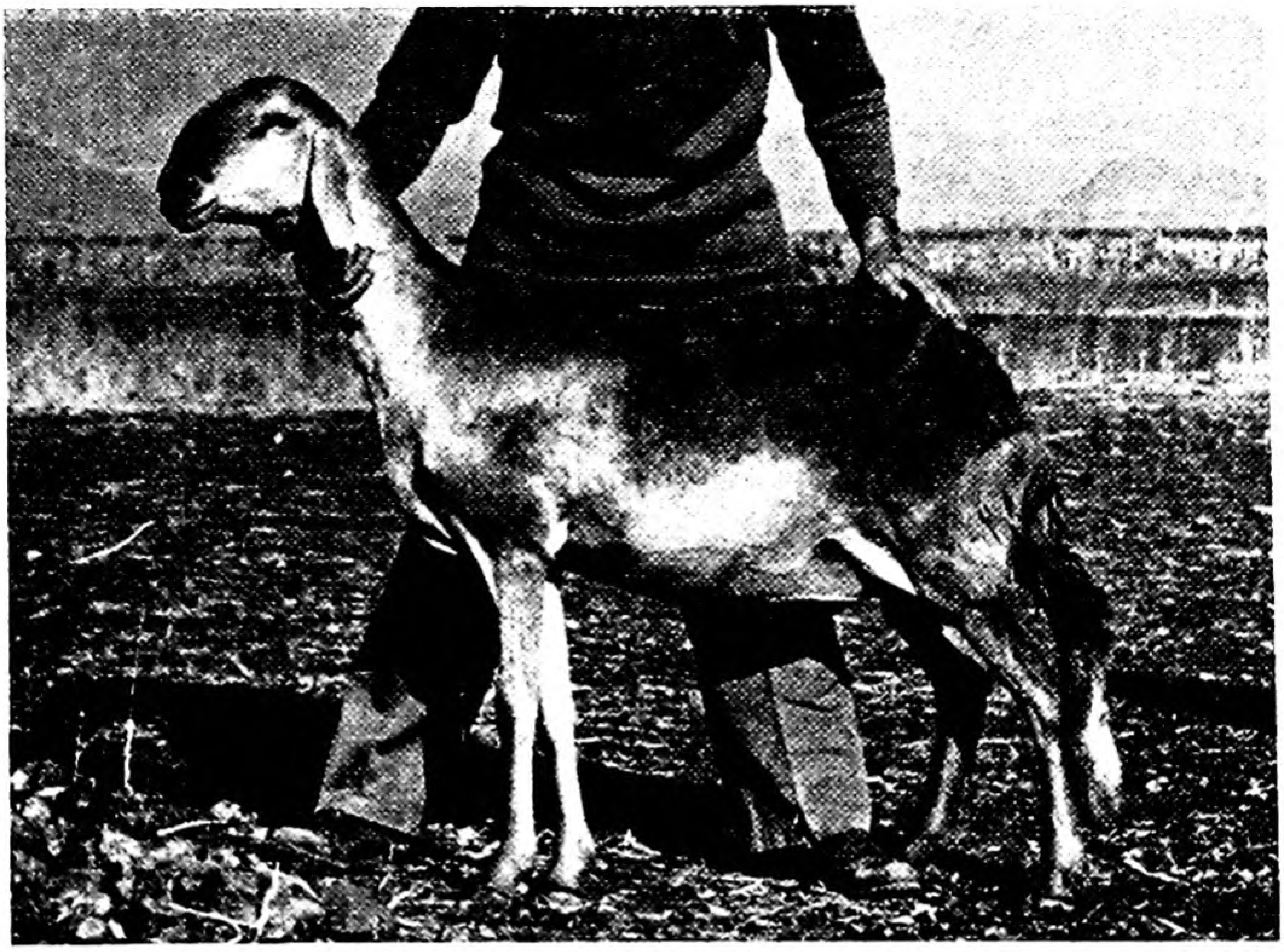


Figure 5.17. Sudanese (Desert) sheep (Tessenei, Eritrean-Sudan border).

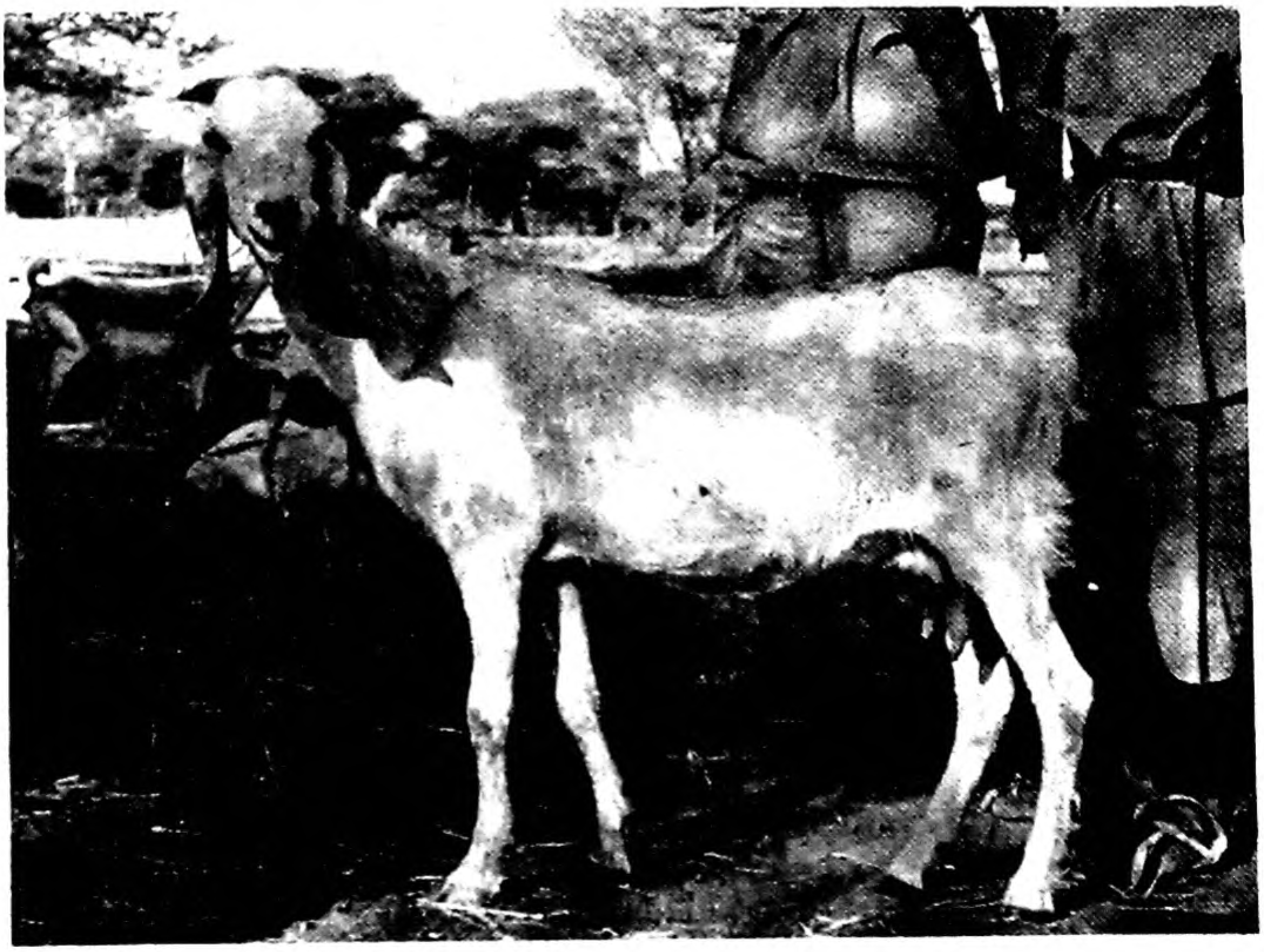
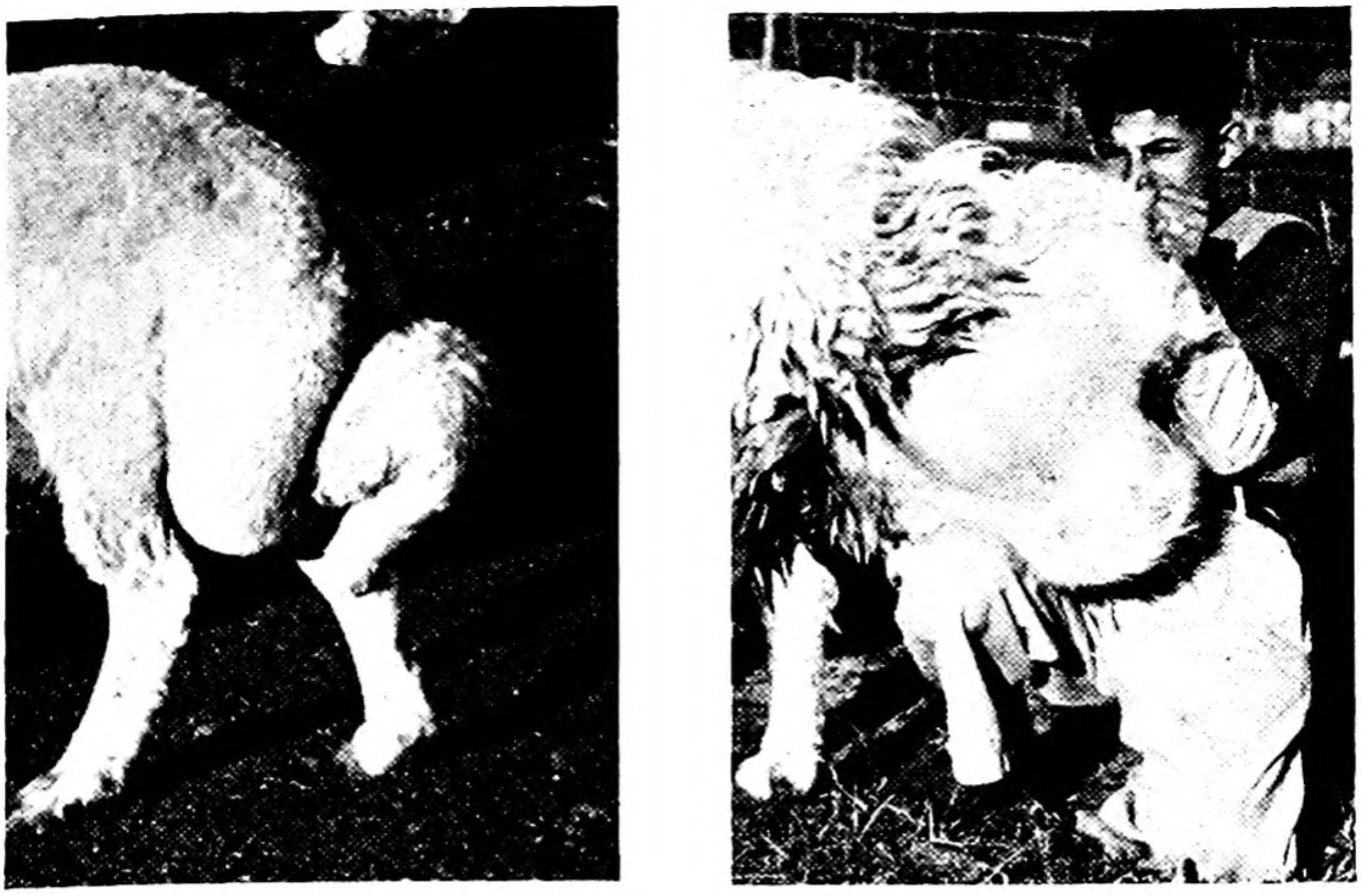
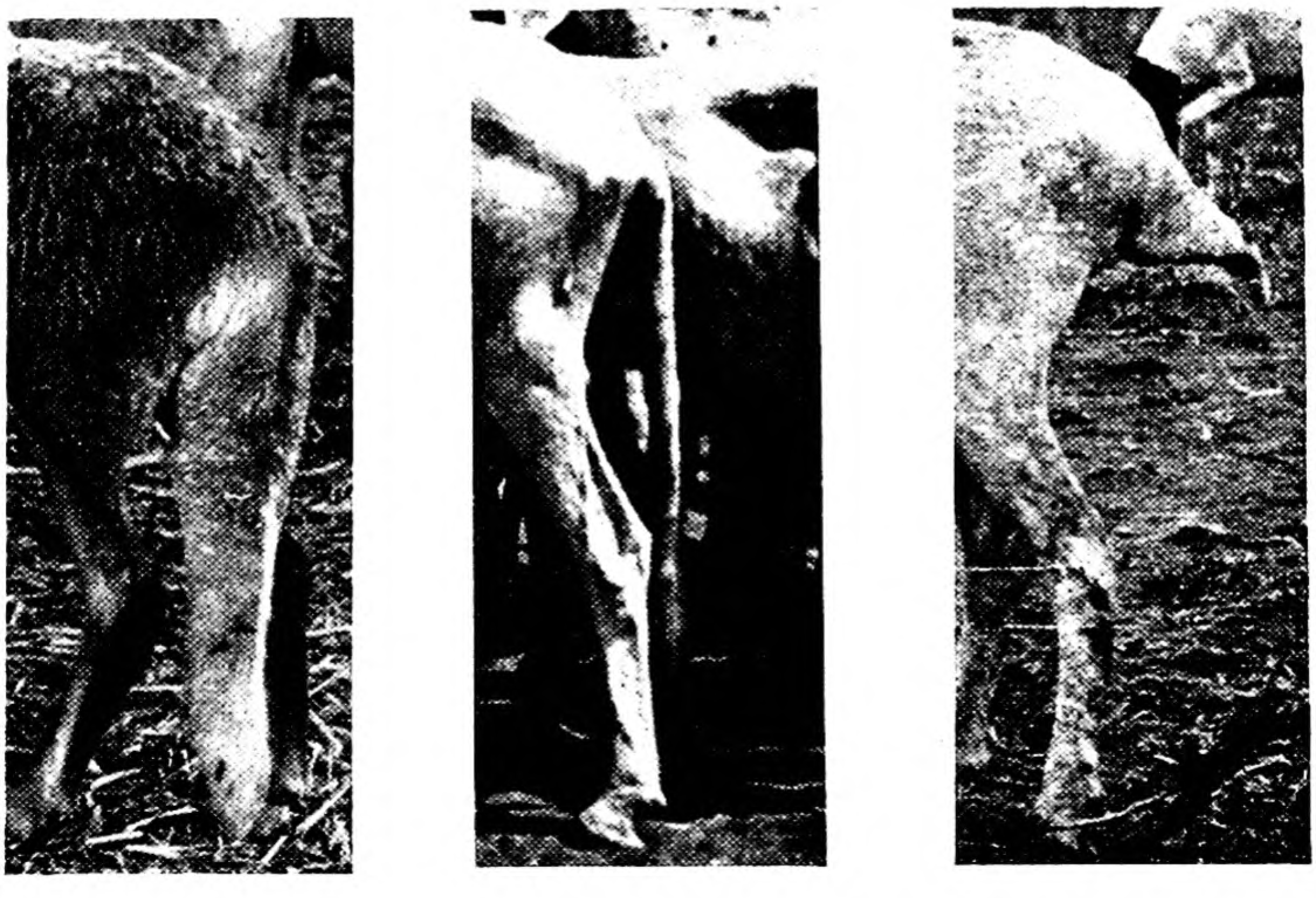


Figure 5.18. Sudanese (Desert) goat (near Cheren, Eritrea).



(*a*) Dorsal surface. (*b*) Ventral surface.

Figure 5.19. Short fat-tail of Northern Desert (woolled) sheep.



(*a*) Long fat-tail, enlarged with fat after the rains.

(*b*) Long fat-tail, devoid of fat after drought.

(*c*) Rump and tail of fat-rumped Somali sheep.

Figure 5.20. Fat-tails of Southern Desert (haired) sheep.

The conformation of both types of desert sheep does, however, differ in one outstanding respect from that of desert goats, *i.e.* in the development of an enlarged fat tail or rump. The function of this fat reserve has already been referred to. It takes a variety of different forms in sheep of different breeds and types. In the sheep of the northern deserts it is usually short and lobed and may extend over the whole width of the body (*Figure 5.19a*). Its undersurface is bare, and in size it may after the rains attain a weight of as much as 10 to 15 lb. (*Figure 5.19b*). With the haired sheep of the southern deserts the tail is long and space is available for fat deposition in the broadened apex as well as in the body of the tail itself (*Figure 5.20a*). At the end of the dry season, when the fat reserve has been exhausted, such a tail may take the form of a long thin rope, devoid of flesh or fat (*Figure 5.20b*). Alternatively (as in the Blackhead Persian or Somali type) deposition of fat may take place on the rump, the tail proper being limited to a relatively small twin-flanged appendage (*Figure 5.20c*). It may be noted that comparable gradations in fat-tailed development have been noted in Eastern Asia and are admirably illustrated in a report by Phillips (1948)

The need for a substantial fat reserve in the desert sheep is obvious, though the reasons for the striking structural differences in the tail itself do not appear to have been studied. Nor is there any clear explanation why, if the sheep requires a specialized fat reserve, the goat (which frequently inhabits the same dry areas) can maintain life and even productivity without one—unless this is associated with its distinctive browsing and rooting habits. As in the comparison between zebu and Sanga cattle there is, however, little doubt that, since the sheep and goat of the hot desert areas are equally heat tolerant, the fattened tails and rumps of sheep, while of great functional significance to their existence in their natural habitat, can have at best only a minor relationship to their heat tolerance.

EQUINES

Any attempt to study the ecology of equines on the basis of their present distribution is inevitably misleading since breeds now universally accepted as of temperate type (*e.g.* the English thoroughbred) actually owe their origin to extensive cross-breeding with animals from hotter climates, notably the Arab. On the other hand to compare, for example, a heavy European breed such as the Shire, which is a pure bred northern type, with the Arab would be to contrast an animal bred primarily for heavy draught purposes with one developed predominantly for speed of movement. Nevertheless even a comparison of this nature is suggestive, since it indicates the tendencies of the two types to develop towards weight and compactness of limb on the one hand and lightness

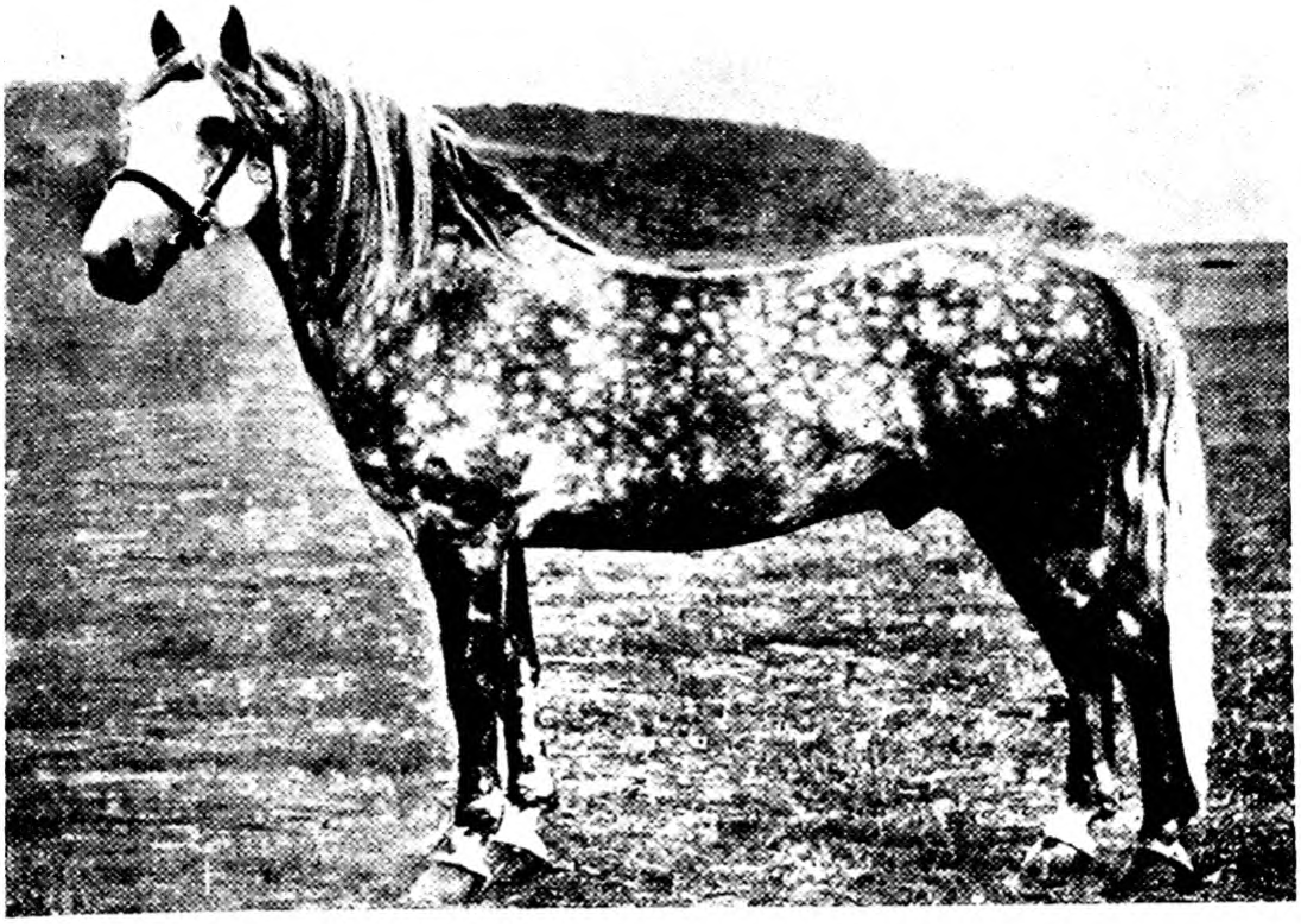


Figure 5.21. Highland pony stallion (Western Islands, Scotland).

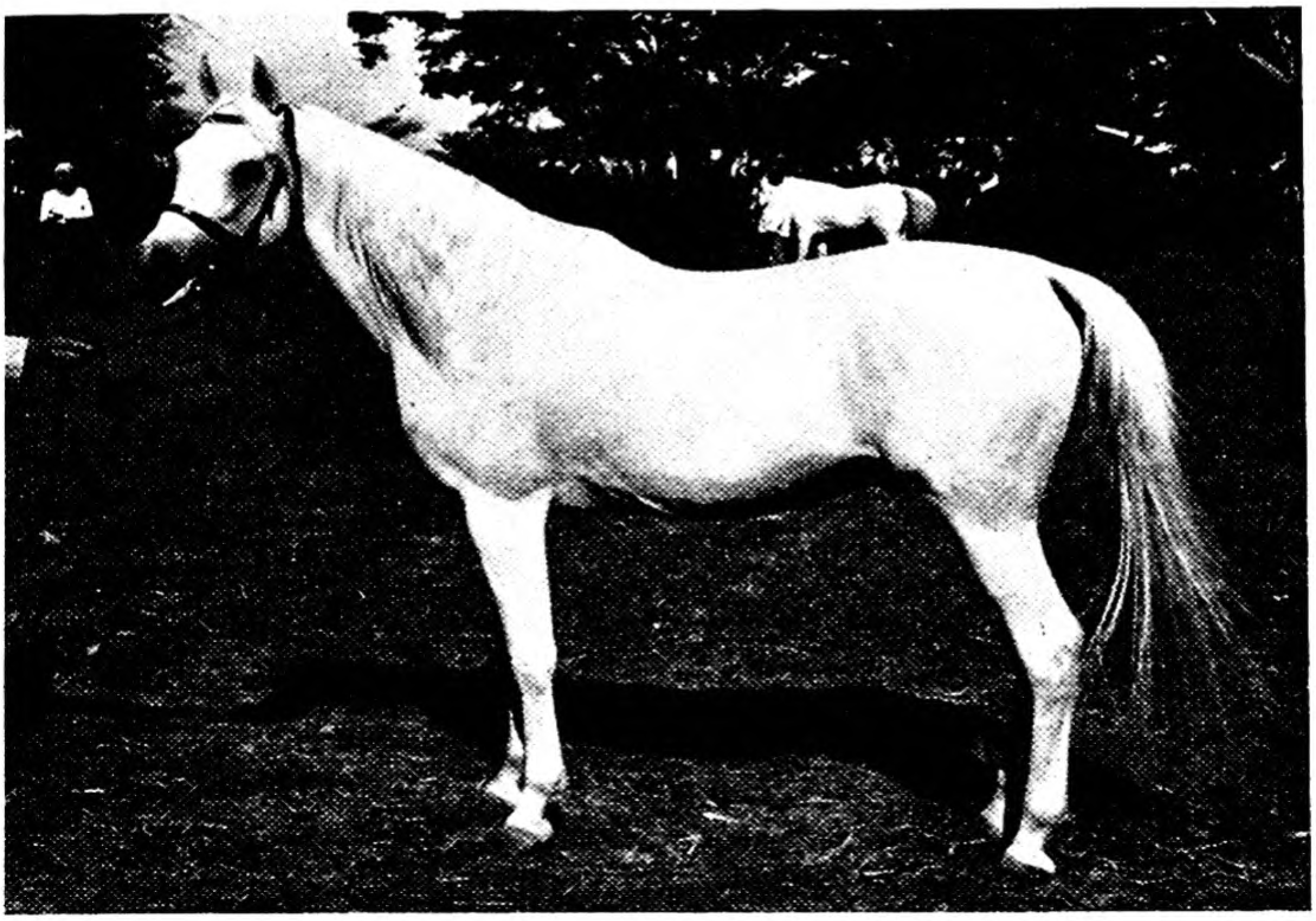


Figure 5.22. Arab stallion (Royal Agricultural Society's Stud, Cairo, Egypt).

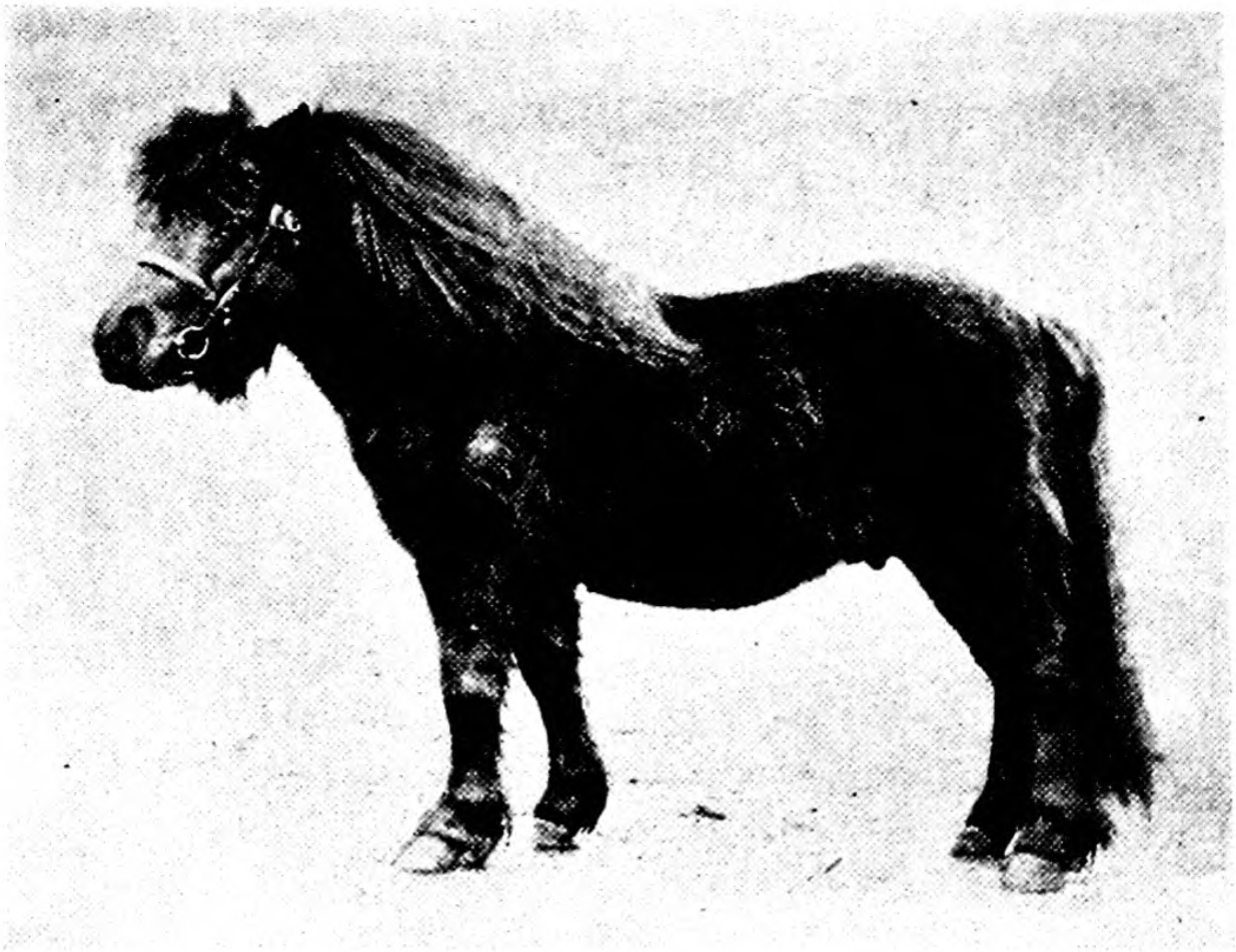


Figure 5.23. Shetland pony stallion (Shetland Islands, Scotland).

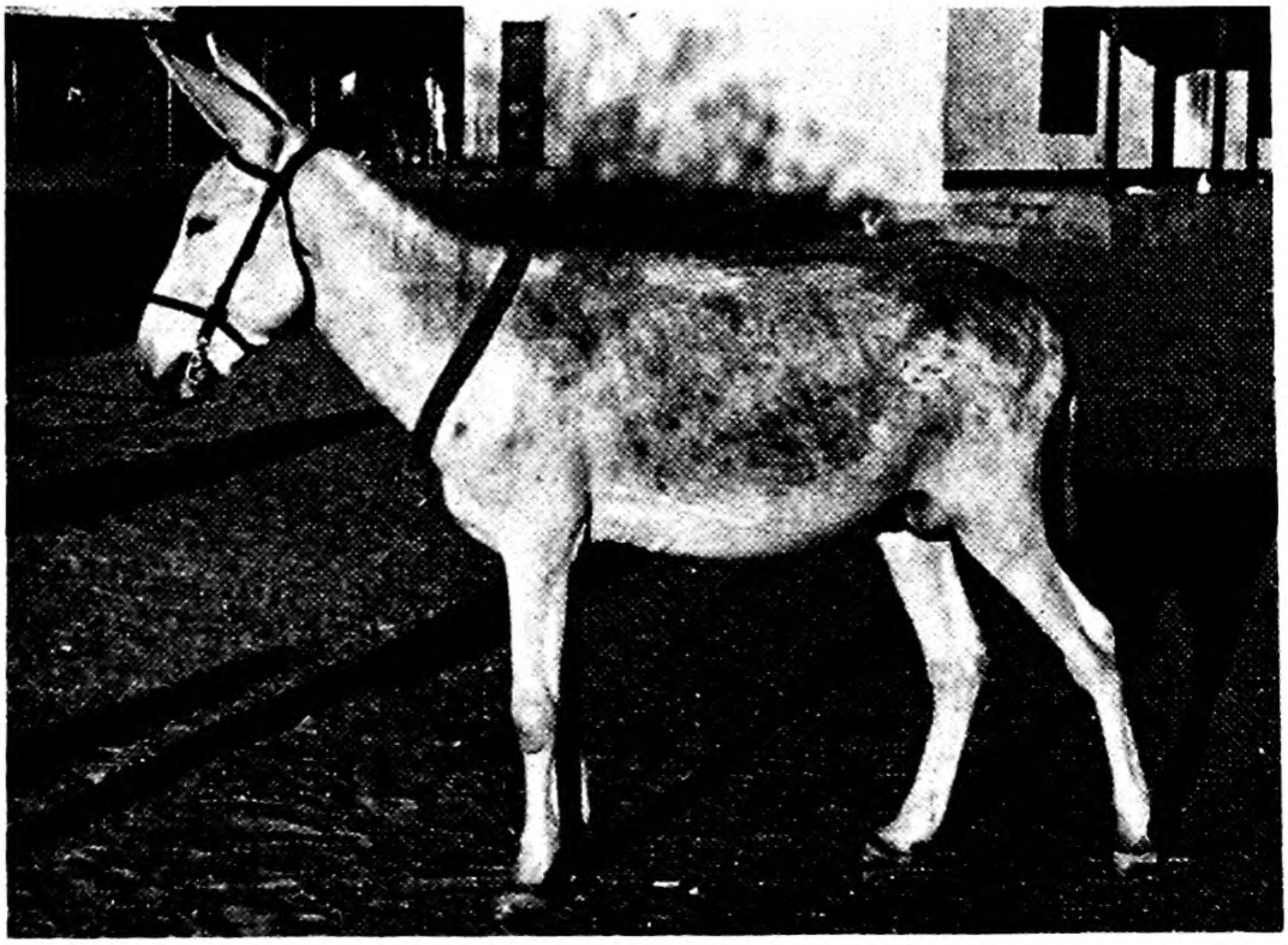


Figure 5.24. Abyssinian jackass (El Obeid, Anglo-Egyptian Sudan).

and length of peripherae on the other (what WATSON and MORE (1944) have characterized as the differences between the " western heavy-legged type " and the " oriental light-legged type "). From this aspect it is incidentally interesting to note that, whereas for the development of speed the more northern countries have had to import southern stock, the importation of heavy northern breeds into the more southern areas has seldom been successfully achieved; where animals are required in such areas for heavy draught purposes it is more usual to rely on mules.

A fairer ecological comparison between northern and southern types would be that between the British Highland pony (*Figure 5.21*) and the Arab (*Figure 5.22*). The former has been maintained in practically pure strain over many generations. It contains some of the largest animals of its type in northern Europe (individual animals may attain a height of 14 hands), and bears a close resemblance to the Eastern Asiatic breeds of the parallel latitudes of Northern China (Phillips, Johnson and Moyer, 1945). Apart from size, it shows, in comparison with the Arab, the same differences in conformation as those found with other classes of northern livestock, *i.e.* a more compact body, a thicker neck and shorter and heavier extremities. Moreover the coat covering of the Highland pony (and to a somewhat less marked degree of the heavier northern draught horse) is thicker, longer and rougher than that of the Arab, which exhibits the typical sheen of the zebu. These differences in conformation and coat covering are exhibited in their most extreme form by comparing the northern Shetland pony (*Figure 5.23*), an animal inured to a cold and bleak environment, with the desert ass (*Figure 5.24*), which is the most typical equine of the hotter southern areas and which (as noted earlier) virtually displaces the horse throughout the tropics and subtropics. Apart from the extreme length of leg in comparison with the body size, and the very fine nature of the hair covering, the ass shows in extreme form the larger ears which are so typical of practically all classes of tropical livestock.

CAMELS

Although, like horses, camels vary widely in their uses (*e.g.* for riding, for transport and for agriculture) and therefore in their detailed conformation, it is possible on the basis of their geographical distribution to differentiate them climatically into two quite distinct types, the two-humped Bactrian camel typical of the colder desert areas of northern Asia (*Figure 5.25*), and the single-humped Arabian camel which is widely distributed over the hot desert regions of Africa and southern Asia (*Figure 5.26*). It would therefore be expected that they would furnish the clearest cut examples of the effects of climate on form and function. The differences in size, conformation and body covering are in fact most marked (Leese, 1927). As regards size, the Bactrian

Figure 5.25. Bactrian camel (Takla Makan, Turkestan) (from "*The Living Animals of the World*" by courtesy, Hutchinson).

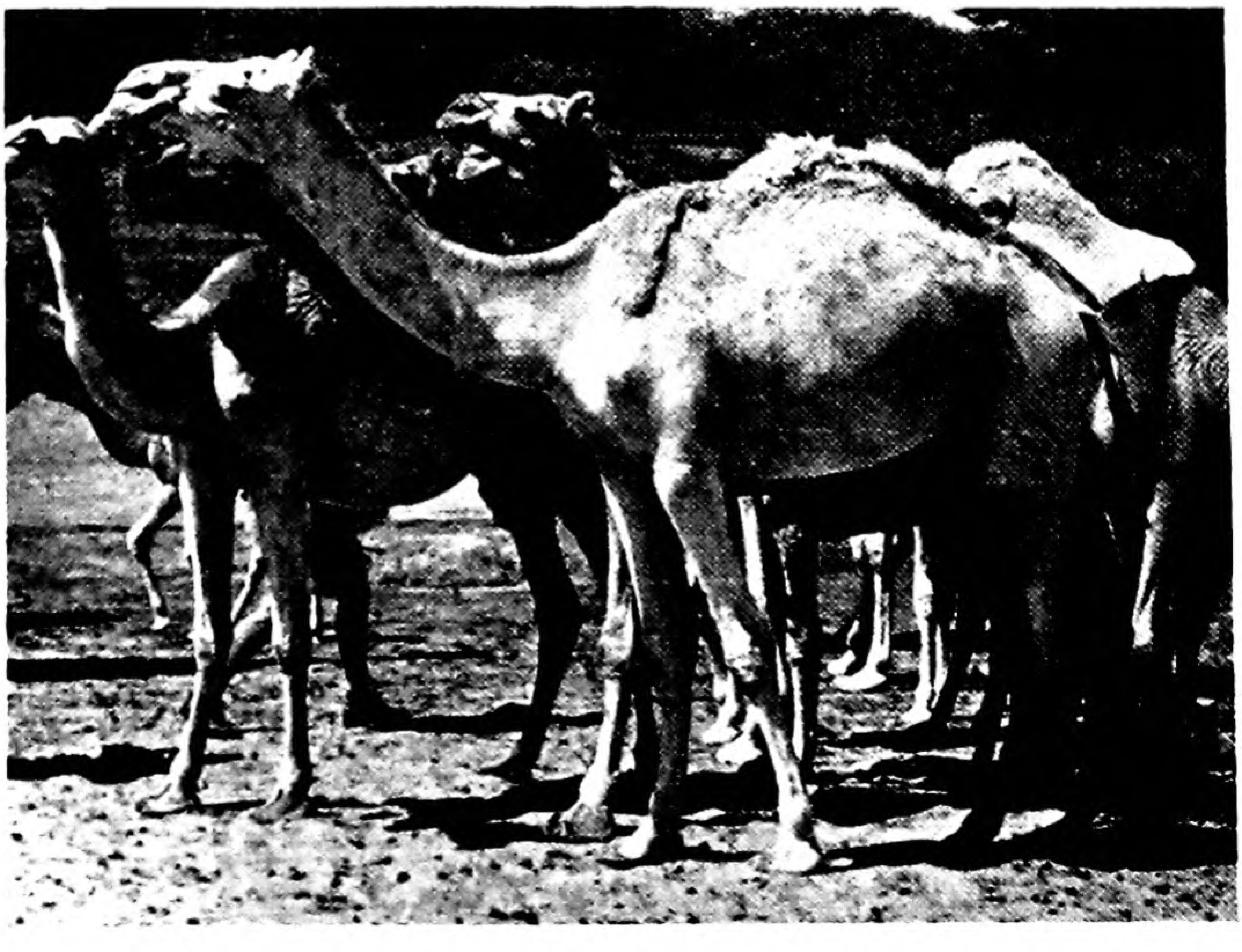


Figure 5.26. Arabian camel (Abbaseyeh, Anglo-Egyptian Sudan).

camel is substantially heavier than the Arabian. Indeed even among Arabian camels those in the more northern areas of India and Afghanistan are heavier than those bred in the hotter areas of the Sudan and of Somaliland. As regards conformation the differences are still more striking. The Bactrian camel is compact, thick set and relatively short-legged; the Arabian camel is less heavily built, is longer and thinner necked and extremely long in the leg. As regards body covering the Bactrian camel has a heavy coat of long coarse hair, specially thick over the head, neck, forelegs and hump. Although in summer this coat is shed in patches, the amount of hair always greatly exceeds that of the Arabian camel; the coat of the latter is in fact not only softer but both thinner and shorter at all seasons.

Moreover, while the colour of the Bactrian camel is dark or russet brown, that of the Arabian camel usually varies from sandy-grey to dirty white. Such, briefly, are the salient differences of the two types—apart from the conformation of the hump, the function of which requires no elaboration.

GENERAL APPLICABILITY OF PRINCIPLES

This necessarily brief description of some of the main characteristics of the more extreme types of the world's livestock will nevertheless serve to indicate how far the general principles discussed in the preceding section are applicable to domesticated animals.

As regards body size, the conditions of domestication vary so widely that it is difficult to demonstrate with certainty the existence of a climatic gradient which conforms to Bergmann's Rule. There seems no doubt that the rule holds good for camels (whose environment has been least affected by domestication) and in general tendency for equines. In regard to cattle its most obvious application is in the dwarfing of zebus and buffaloes in the hot-wet tropics though the question must remain open as to whether, as WRIGHT (1946) has suggested, this is a direct climatic effect (*i.e.* associated with the relatively larger surface area of the body) or whether the effect is only indirectly related to the climate through inadequacies in the quality of the local vegetation (HAMMOND, 1947).

On the other hand as regards conformation there is no doubt that practically all classes of domesticated livestock conform to Allen's Rule in possessing, in the hotter climates, less compact bodies with enlarged peripherae and hence larger surface areas per unit of body weight. While this is clearly seen in the length of leg, the length and fineness of the neck and the size of ears of most species, it is most strikingly illustrated in the enlargement of the dewlap and sheath of sub-tropical and zebu cattle—a modification in conformation which has been estimated by KIBLER and BRODY (1950) to increase the surface area of the body by as much as 12 per cent. Moreover in relation to an animal's potentialities for loss of body heat by radiation, it is significant that these additional areas of loose skin all either face the ground or can be shaded by the body (as shown strikingly in *Figure 5.5*)—a feature which might be expected to facilitate heat dissipation in an unshaded environment. It is also significant in this connexion that in certain types of desert sheep it is (as already noted) the *ventral* surface which is free from hair.

Turning to the body covering in general, Wilson's Rule regarding the thickness and nature of the coat cover is also substantiated in every class of stock. In respect of cattle this rule has in fact received detailed confirmation in Bonsma's (1943) finding that not only do heat tolerant animals possess glossy coats of short fine hair, but that the less heat tolerant types with dull and sheenless coats have both a protective covering of long straight hair and an undercoating of warmth-retaining woolly fibres. This observation has been amplified by FRENCH (1946) who found not only a difference in the type of coat but also in the rate of growth of hair. Bonsma's conclusion regarding the significance of the thickness of the skin is more open to question. Such an increase in thickness has been found by THOMSON (1946) to be particularly marked in cattle inhabiting marshy areas (as in the Sanga cattle of the Upper Nile swamps), where it is stated to protect the animal from fly worry and insect attack. Indeed, this is held by Thomson to be one reason why the thinner skinned Arab cattle—while possessing adequate heat tolerance—cannot be successfully introduced into the upper reaches of the river (BENNETT *et al*, 1948). There seems, too, little doubt but that it is the thickened skin of the buffalo which enables this animal to thrive in hot and marshy areas. Until more information is available, not only in regard to cattle but to the other classes of stock described in this section, the true significance of skin thickness as a protection against the direct effects of climate (*i.e.* against insolation) cannot, however, be assessed.

Finally in regard to colour, observations on the skin pigmentation of cattle indicate the gradual darkening with increasing temperature and humidity which is implicit in Gloger's Rule; indeed the jet black pigmentation of both cattle and buffaloes in the hot-wet tropics provide a striking confirmation of his thesis. With other species reliable data are unfortunately almost completely lacking from the literature. Hair colour, unlike skin colour, appears however to be governed by far more complex genetic factors, and cannot be linked with any climatic gradient. White, red, black and multi-coloured animals are inextricably mixed in all climatic zones, and it can only be assumed that the origins of the present types and breeds have themselves been so diverse, and their migrations so widespread, that any original colour gradient which may at one time have existed has now become completely masked. Nor is there, incidentally, any regular climatic gradient in the length of horns such as Allen (1877) claimed to have observed: animals in north and south may equally be polled, short, long or lyre-horned.

Apart from the coat colour and the horns, this brief discussion will, however, serve to indicate that the earlier enunciated principles governing form, function and distribution are in fact applicable to the world's main livestock types.

IMPORTANCE OF LOCAL VARIATIONS IN TYPE AND BREED

The foregoing illustrations have been selected as extreme examples of the effects of climate on the characteristics of different types of livestock. But it would be incorrect to assume that the general principles apply only to comparisons between widely spaced regions and widely divergent climatic conditions. Bergmann (1847) stated clearly in his original paper that a gradual change in latitude, and therefore in environmental temperature, was accompanied by an equally gradual change in body size. Allen (1877) similarly postulated (and demonstrated with the mammals which he studied) that there was a gradual increase in the size of the body peripherae with increasing environmental temperatures. Wilson (1854) was no less definite in stating that the nature and abundance of the coat cover was " in inverse ratio to the temperature of the locality ", while Gloger (1833) implied the existence of a general correlation (which carries with it the implications of a gradual adjustment) between pigmentation and the warmer and more humid climates on the one hand and the cooler and drier climates on the other. There would therefore seem to be every reason to anticipate (and this anticipation has been confirmed in detailed regional livestock surveys) that there will normally be no sudden changes in the forms and functions of domesticated livestock (except where some insuperable physical barrier happens to separate two diverse climatic areas), but that the characteristics typical of each successive zone will merge with those of its neighbours almost imperceptibly—this being facilitated by interbreeding at the zonal boundaries. Such gradual merging is not only true of, say, cattle where, to take an obvious example, the conformation and coat cover of the northern European types show gradual modifications, as one goes south, first towards those of the Mediterranean types, and then progressively towards those of the sub-tropical types of North Africa and the Middle East. It is equally true of the gradual development of the fat-tail in the sheep as one passes from the sparse seasonal herbage of south-eastern Europe to the desert areas of Asia Minor and beyond, and, as Phillips (1948) has shown so convincingly in comparative illustrations, of parallel developments in sheep inhabiting China. And it is, to take a more extreme example, true even of the camel which, starting as the light Arabian type in Somaliland and the Sudan, gradually increases in size and weight and—at its boundary with the heavier two-humped Bactrian camel—actually crossbreeds (Leese, 1927).

While these gradual adjustments in form and function represent natural adaptations to a continuous sequence of changing environments, other modifications may result either from the intentional introduction of imported stock or from more casual interbreeding with migrant herds and flocks. In consequence, specific local variants or breeds are, in the course of time, likely to be produced, each possessing individual characteristics suited both to the local climate and to the economic and social needs of the area. The number of such local variants or breeds is surprisingly large; MASON (1951), in an invaluable world dictionary of livestock types, lists as "recognized breeds" (*i.e.* breeds either possessing herdbooks, or recognized as such by an appropriate local authority, or comprising uniform true-breeding populations) no less than 250 breeds of cattle, over 200 breeds of sheep and (to take a particularly striking example) some 60 breeds of goat. The occurrence of such localized breeds in Britain and other European countries has long been recognized, and DAVIDSON (1927) and JOHNSON (1924) have shown the existence of generalized stratifications of both cattle and sheep breeds in North America. In Africa, owing to the extensive original migrations of stock (CURSON and THORNTON, 1936; BELLINI, 1941) and to the widespread practice of nomadic husbandry, many of the existing types are of very mixed origin, but there are, nevertheless, large localized pockets of fairly uniform stock (SIDKY, 1951 and 1951/53; FAULKNER and BROWN, 1953, Appendix XIII). This applies not only to breeds of cattle but also to a more limited extent to sheep and goats (MARCHI, 1929; Bennett *et al*, 1948). In Western Asia distinct breeds of cattle, sheep and goats have been described and named in many areas (HIRSCH, 1932 and 1933; WILLIAMSON, 1949), though there is undoubtedly some overlapping in nomenclature which Mason (1951) has fortunately disentangled. In India in particular substantial progress has been made over the last two decades in defining the main characteristics of local breeds of cattle (OLVER, 1938; WARE, 1939, 1942; JOSHI and PHILLIPS, 1953). Moreover in India and certain countries of the Middle East and of East Africa, as well as in the more highly developed Western countries, great strides have been made in raising the productivity of such breeds, which are therefore potentially available for introduction as improved stock into less advanced areas.

The characteristics of these various types and breeds have, however, usually been developed within relatively circumscribed localities, and their morphological and functional adaptations will thus be primarily suited to their own particular climate and environment. Where therefore it is proposed to transfer them to other areas for improvement purposes, it is clearly essential that reliable methods should be available to assess their fitness for their new surroundings.

DETERMINATION OF THE SUITABILITY OF LIVESTOCK FOR INTRODUCTION INTO NEW AREAS

It is obvious that, in selecting animals for introduction into new areas, the criteria of suitability cannot be limited to their physiological reactions to the local climate and environment. It is no less important that they should be capable of meeting the economic and social needs of the human population. Thus, as the Royal Commission on India (1928) pointed out, it would be fatal to the development of Indian agriculture if, for example, the excellent draught qualities of Indian cattle were to be sacrificed in an attempt to raise their milking potentialities. Similarly animals introduced to improve the heat tolerance of, say, Texas cattle ought to possess potentialities for meat production, while those introduced into the vicinity of urban centres should be selected for their milk producing qualities. The same point holds, of course, with sheep. Those in Britain are bred primarily for meat production in order to meet the needs of a highly urbanized population; on the other hand in Australia, where extensive grazing areas are available and the local population is relatively sparse, wool production is economic. Moreover even within individual commodities such as wool, it is necessary to take into account specialized requirements. Thus Australia needs sheep which furnish fine fleeces for its international trade, while Persia requires coarser woolled types which form the foundation of its world famed carpet industry and (from the fat-tailed Karakul) of its production of black (Astrakhan) and grey Persian lambskins.

Apart from their ability to meet such specialized economic and social requirements, it is no less essential that introduced stock should be immune or at least tolerant to the diseases which are prevalent in their new areas; the devastating effects of tick-borne infections (and even of foot-and-mouth disease) on European stock imported into tropical areas form a grim warning of results of neglecting this precaution.

While these wider considerations (which have been reviewed in detail by WRIGHT, 1936 and 1947) are of obvious practical importance in determining the suitability of livestock for importation into new areas, they fall largely outside the scope of the present book, which is primarily concerned with the more purely physiological reactions of domesticated animals. From this latter aspect it is the climatic environment which is important, first in respect of its direct relationship to heat tolerance, and second because of its influence on nutrition *via* the local vegetation. The factors which are directly related to heat tolerance are environmental temperature, solar radiation, humidity and air movement. In regard to vegetation the most important single factor is the rainfall. It will be convenient first to deal with each of these factors separately and then to indicate how they can best be combined as general indices of climatic suitability.

INDIVIDUAL CLIMATIC FACTORS

Environmental Temperature

In the past most methods of temperature classification have been based on its influence on vegetation. Thus SUPAN (1896) divided hot and cold climates into those with mean annual isotherms above 20°C (68°F) and below 10°C (50°F). These two basic figures were adopted by KOPPEN (1923) in his more detailed classification; they have been modified by Miller (1947), who prefers the figures of 70°F and 43°F as being the limits for the growth of palms and for the boundary between broad-leaved evergreen and broad-leaved deciduous forests respectively. Although such criteria have little or no direct relationship to the reactions of livestock to environmental temperature, it will be shown in Chapter 6 that from the point of view of heat tolerance the figure of about 70°F does appear to provide a rough critical borderline between temperate and other stock. It might be assumed, therefore, that a temperature classification based on, say, the mean annual isotherm of 70°F, supplemented perhaps by a series of isopleths indicating the maintenance of this temperature for varying periods throughout the year, would furnish a suitable basis for classifying animal environments. Such an arbitrary basis would, however, fail to take into account the very wide *ranges* in temperature which occur in different localities even when these lie on the same isotherm or isopleth. Thus while in the low-lying hot-wet areas (particularly on the coasts) and at high altitudes in the tropics there is usually only a mean monthly range of 5° to 6°F, in hot and cold desert areas there may be variations ranging from 30°F to as much as 80°F between the coldest and hottest month. Moreover such seasonal differences in temperature range are paralleled in diurnal differences; in the hot-wet tropics the temperature variations between day and night are usually small; on the other hand in desert areas they may be such as to result in midday conditions which are unbearably hot, with nights sufficiently cold to cause dew pools. Such marked variations in temperature (which may well affect the physiological reactions of livestock, *e.g.* by providing ' recovery ' periods in the cooler months or the cooler nights) indicate that the mean annual temperature cannot itself be used as a satisfactory index for assessing the suitability of an area for a given type of livestock; due weight must also be given to the seasonal (and parallel diurnal) variations about that mean.

Solar Radiation

The intensity of the solar radiation will clearly affect the suitability of an area for a given type of livestock, not only on account of its close relationship to the environmental temperature but (as noted in connexion with skin pigmentation and possibly thickness) in relation to its direct effects on the body covering. Unfortunately few meteorological stations appear to possess facilities for the measurement of solar radiation (or to publish such data if available) so that for practical purposes it is seldom that this factor can itself be taken into account in assessing the local climate. In general the intensity of radiation appears, however, to be fairly closely related on the one hand to the air temperature and on the other to the cloudiness and therefore to the rainfall. It is thus likely to be relatively high in desert areas and relatively low in areas of high rainfall. In addition the latter areas will probably furnish more abundant natural shade than the former. Moreover, even if accurate information regarding the intensity of solar radiation were available, its interpretation in terms of animal physiology and heat tolerance would, owing to the present lack of fundamental knowledge of the subject, be virtually impracticable. It appears therefore that, provided allowance is made in any combined climatic index for both air temperature and rainfall (or a function of the two such as humidity), solar radiation *per se* can probably be neglected in any practical climatic classification though (as will be clear from Chapter 6) its importance from the fundamental aspect cannot be too greatly stressed. It should be added that the diurnal variations in solar radiation, in the sense of the relative periods of daylight, do have very significant physiological effects, particularly in relation to the sexual cycle. This subject will be dealt with in detail in Chapter 8.

Humidity

The relation of humidity to the suitability of the climate for any given livestock type will clearly depend on the extent to which evaporation from the body surface forms part of the heat-regulating mechanism. There appears no doubt that, in regard to cattle, surface evaporation is a very important factor; at high temperatures THOMPSON, MCCROSKEY and BRODY (1949) have found that it accounts for more than half the total heat loss. Apart from cattle, little information is available, though it is assumed that with animals possessing a thicker body covering (notably with sheep) evaporative losses from the body surface may be of less significance owing to the entrapping of moisture in the wool mesh (FINDLAY, 1950). Nevertheless the significance of surface evaporation in such an important class of stock as cattle (and probably in certain other more lightly covered animals) indicates that humidity measurements must be included in any practical assessment of climatic suitability.

Since the humidity reflects the moisture content of the air, it might be assumed that it would run parallel with the rainfall and that its separate measurement should therefore be unnecessary. This would overlook the fact that it is also markedly affected by the presence of large natural areas of water (*e.g.* even in otherwise desert regions it tends to be relatively high both in coastal areas and in the vicinity of inland lakes), that it is similarly affected by large scale artificial irrigation, and that it may also be influenced to a marked degree by the nature of the terrain. The separation of humidity from rainfall in climatic classifications of livestock (and certainly of cattle) appears therefore to be fully justified. The method of expressing humidity does, however, raise certain difficulties. In the first place there is some difference of opinion as to whether, for physiological purposes, it should be expressed in absolute or relative terms. LEE (1949) considers that in relation to heat loss in animals it is the absolute humidity which is significant. On the other hand it is usual in standard climatological tables to record the relative humidity, and this also coincides with its customary use in ventilation and similar studies. Moreover, as will be shown later, this is the form in which it can be most conveniently incorporated into climographs. In the second place if the relative humidity is used, it must be recognized that it is subject to extremely wide diurnal variations. It is essential therefore that all comparisons should be made on an identical basis. Where possible a 24-hour mean should be used; the nearest approximation to this is usually the mean of two readings taken at the periods of maximum and minimum temperature, or at least at 10 to 12 hour intervals. If, however, reliance has to be placed on single readings, it is physiologically more important to compare those for the hottest time of the day, since this represents the period when an animal's heat tolerance is most severely strained. In the third place, the relative humidity shows wide seasonal variations. Since the pattern of these variations will affect the reactions of livestock (for clearly a high humidity in a hot season will call for greater heat tolerance than in a cool season), it is obvious that (as with air temperature) a mean annual figure would be of little significance; in any assessment of climate the seasonal variations must also be clearly indicated.

Air Movement

In assessing the cooling capacity of the air in relation to heat tolerance the speed of air movement is naturally an important factor, not only in relation to heat loss by convection but even more through its effect on evaporative cooling from the skin. As with solar radiation, however, few standard climatological tables furnish adequate records of air movement. Moreover even such sparse records as exist would be difficult to apply except within a very circumscribed area, since air movement is apt to be extremely localized. Fortunately the general character of air movement can be roughly correlated with certain more general climatic characteristics. Thus in hot-dry conditions, which are typical of the desert areas, air movement is considerable, not only because of the effects of the heating of the unshaded ground but because of the sparseness of larger vegetation. On the other hand in hot-wet conditions, where the predominant vegetation is frequently dense jungle, air movement is reduced to a minimum. In practice, therefore, the disadvantage of the lack of extensive air movement data is likely to be more apparent than real, provided data for temperature, rainfall and/or humidity are available.

Rainfall

Rainfall is well known to be of very limited importance in respect of its direct influence on the animal body, though it has in certain instances been recorded as exerting an advantageous cooling effect (MINETT, 1947). Those animals to which such a cooling effect might be disadvantageous (*e.g.* in cold climates) usually possess a body covering which mitigates the danger. It is in its indirect effects in influencing the nature and profuseness of the vegetation that it is of supreme importance. It would be out of place to discuss here the large number of climatic types which result from differences in the quantity and seasonality of the rainfall; details can be found in any standard work on climatology such as that of Miller (1947). It will suffice to note the significance of seasonal droughts in relation to nomadic husbandry (and hence to the form and distribution of livestock in desert and semi-arid areas) and the marked differences effected by summer, winter and all-the-year-round rainfall on the character and seasonality of the natural herbage and therefore on the sexual cycle, the breeding habits and the rate and form of growth of the local stock. It is self-evident in the light of such differences that, again as with temperature, it is essential in determining the suitability of an area for a given class of stock to examine not only the total annual rainfall but more especially its seasonal distribution.

METHODS OF SELECTING HOMOCLIMATIC AREAS

It is clear from this brief summary that in determining the climatic suitability of one area for the introduction of stock from another (*i.e.* in determining whether two areas are homoclimatic) only three main factors need—or indeed in practice can—be taken into account. These are the environmental temperature, the relative humidity and the rainfall. It would obviously be convenient if these could be combined into a single index. THORNTHWAITE (1931, 1933) and PRESCOTT (1934) have in fact devised and investigated single value climatic ratios, but these were intended primarily as indices of vegetation and cannot be directly related to heat tolerance in animals. The alternative of using an experimentally determined single figure, such as a dry or wet katathermometer reading (HILL, 1919 and 1923) while attractive in principle, is not only unsupported by any extensive collection of observations (such as are available for temperature, humidity and rainfall in most current climatological tables) but is in fact no longer regarded as an adequate index even for internal ventilation studies (Findlay, 1950). Nor does it appear that, in our present state of knowledge of heat tolerance in animals, the determination of the *effective temperature* (BEDFORD, 1946) or of the *standard operative temperature* (WINSLOW, 1941) could provide either a satisfactory or a practicable single homoclimatic index for livestock.

Two ingenious methods of comparison have, however, been devised, each of which is based on the use of two of the three climatic factors already mentioned and each of which has proved its value under practical field conditions. They are termed respectively the *climograph* and the *hythergraph*. The former is based on the relation of air temperature to relative humidity; it can best be illustrated by application to cattle which, being relatively short haired are (for the reasons already noted) likely to be specially susceptible to changes in humidity. The latter is based on the relation of air temperature to rainfall; since an adequate supply of natural fodder (which will itself be largely influenced by the rainfall) is particularly important to animals which derive their food supplies solely from extensive grazing, it appears that this basis of comparison would be particularly applicable to and best illustrated by reference to sheep—whose thick coat in any event renders them less directly susceptible to changes in the relative humidity. It should be added that the outstanding feature of both the climograph and the hythergraph is that each takes into account not only the individual but also the concurrent seasonal changes in two of the three most important climatic factors.

Climographs

Climographs were originally devised by BALL (1910) and their use has been applied to domesticated animals by SHELFORD (1920), by Johnson (1924) and more recently by Wright (1946). A climograph is constructed by plotting as a single graph the mean monthly air (dry bulb) temperatures against the mean monthly relative humidities. The resulting points are joined to form the climograph, the position, shape and area of which reflects the summated environmental conditions. It will be seen from *Figures 5.27* and *5.28* that the full diagram, within which a series of climographs may be plotted, can be roughly divided into four sections, corresponding respectively to climates which are cold and moist (*raw*), cold and dry (*keen*), hot and moist (*humid*) and hot and dry (*scorching*).

Turning to the application of climographs to cattle, Europe and Asia have been selected to illustrate the climates* typical of the three most extreme types, *i.e.* the temperate European, the large tropical zebu of the Northern Plains of India and Pakistan, and the dwarfed zebu of south west coast of India and of Ceylon (*Figure 5.27*). An examination of this diagram reveals the following facts. (1) The climograph for temperate European cattle falls wholely within the lower right-hand section, *i.e.* the temperature never approaches the critical figure of 70°F and the humidity remains tolerably high throughout the whole year—as would be expected with an adequate and consistent rainfall. The shape of the climograph is regular and it is of moderate size, indicating freedom from climatic extremes without undue seasonal monotony. (2) In contrast the climograph for the large tropical zebu cattle of the Northern Indian Plains falls almost entirely in the upper left-hand section, *i.e.* the temperature lies for all but three months above the critical figure of 70°F, and the humidity is exceptionally

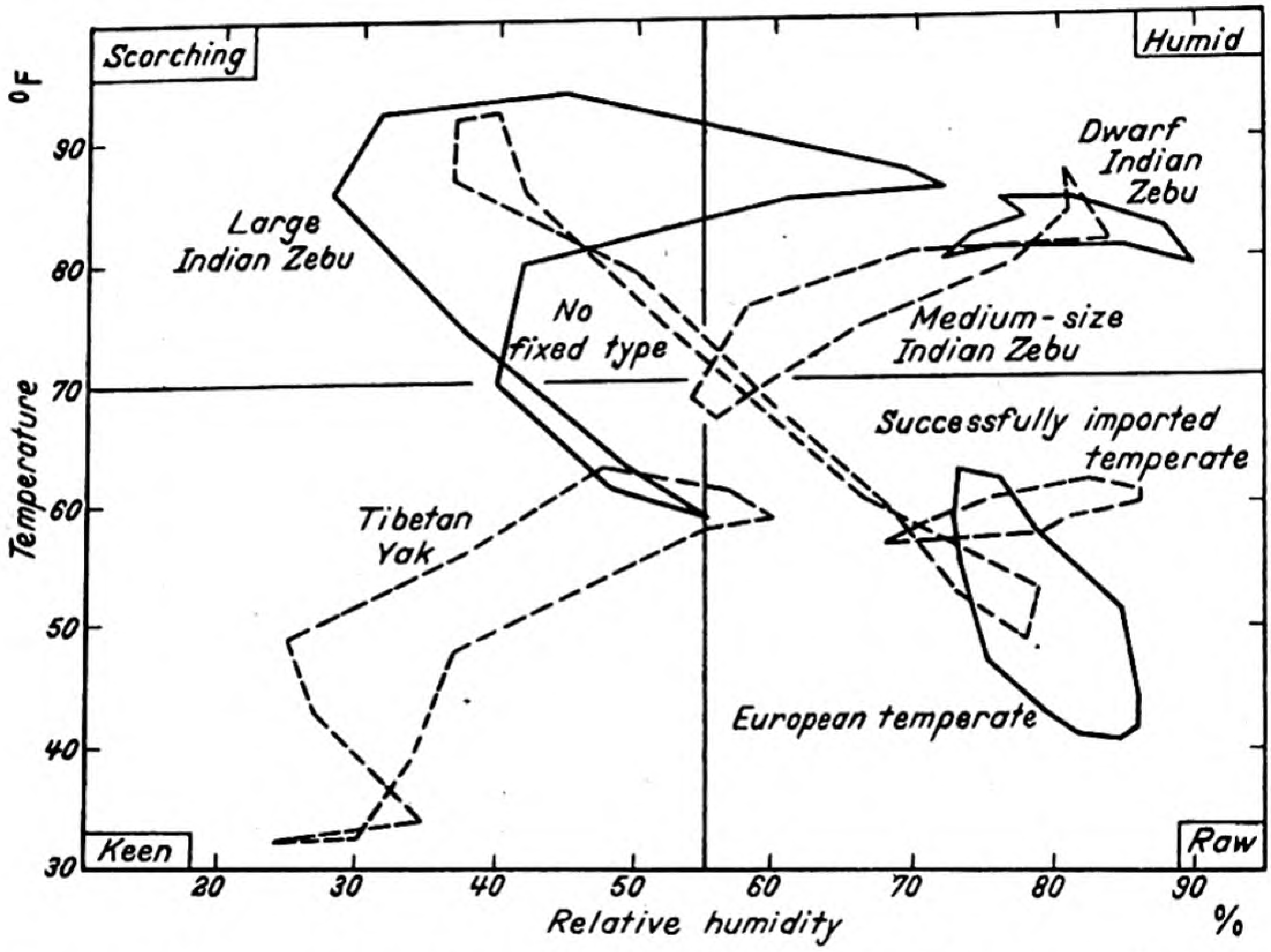


Figure 5.27. Typical climographs for cattle in Europe and Asia. *Details*:—European temperate (London, England); large Indian zebu (Delhi, India); dwarf Indian zebu (Cochin, Southern India); yak (Lhasa, Tibet); successfully imported temperate (Nuwera Eliya, Ceylon); medium size Indian zebu (Karachi, Pakistan); no fixed type (Baghdad, Iraq).

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* The meteorological data on which *Figures 5.27* to *5.31* are based have, unless otherwise stated, been obtained either from the Meteorological Office, London, or from figures published by the Ministry of Public Works, Egypt (1938) or Kendrew (1953). Both temperature and relative humidity values have been adjusted to 24-hour means.

low for all but the monsoon period. This climograph covers, moreover, a large area and is most irregular in shape, indicating wide seasonal variations (and correspondingly wide diurnal fluctuations) throughout the year. (3) Again in contrast, the climograph for the dwarfed zebu cattle of the south-west coastal areas of India falls entirely within the upper right-hand section, *i.e.* the temperature lies for all twelve months well above the 70°F line, while the humidity remains consistently high. The particular characteristics of such 'dwarfing' areas are, in fact, not only their high levels of temperature and humidity, but the almost complete lack of any marked seasonal (or corresponding diurnal) variations in climate—a point clearly apparent from the very small areas of their climographs.

Four other climographs have been included in *Figure 5.27*, partly in confirmation and partly in extension of those already described. The first, that of the Tibetan yak, represents the climatic conditions in certain drier mountain areas at an elevation of 12,000 ft. and with an extremely seasonal rainfall. No great significance should be attached to the figures for the relative humidities at these comparatively low temperatures, since even at saturation the vapour pressure will itself be extremely low (RAGSDALE *et al*, 1953). Nevertheless the natural habitat of the yak will correspond roughly to climographs of this type, though there may in wetter areas be a shift to the right (*i.e.* towards higher relative humidities) or in more northern areas downwards (*i.e.* towards lower winter temperatures). The second, that of cattle in the highest hill station in Ceylon (with an elevation of over 6,000 ft.) typifies the climate of the very limited high altitude areas in the tropics where temperate European cattle have with some success been introduced (Wright, 1946). It is significant that the climograph of this area not only coincides closely with that of the original home of the imported European cattle but that it also coincides with those of the hill stations of Northern India, where the local Indian cattle of the Siri breed are in many ways comparable to European cattle, *i.e.* they have small ears and only a moderate sized dewlap, carry a thick coat all the year round, and possess only a moderate hump of cervico-thoracic (*i.e.* muscular) type rather than of thoracic (*i.e.* fatty) type (Joshi and Phillips, 1953). The third, that of cattle in the north-west coastal desert area of India, indicates the climate of an Indian breed (the Red Sindhi) which appears to possess both size and conformation and heat tolerance intermediate between those of the plains and of the hot-wet tropics—the humidity having been increased over a large part of the year from the normal low figures of the plains and the desert by the combined effects of contiguity to the coast and the heavy monsoon rains. Cattle of this breed (*Figure 5.12*) are (as might be expected from their climograph) held to possess the very valuable asset of wide climatic adaptation (Olver, 1946; Joshi and Phillips, 1953). The fourth, that of the cattle of central Iraq, presents the breeder with an unsolved problem. It will be seen that for half the year the climate is of hot-dry plains or desert type (with seven months over 70°F), while for the remaining half-year it is typical of the cooler temperate zones. The cattle of this area are among the most poorly developed of any in the Middle East, and as yet all efforts (and they have been numerous though limited in scale) to introduce and to crossbreed with temperate or zebu cattle have failed to produce a satisfactory type. Moreover the area itself is so closely situated to the normal migratory routes between east and west that its past history (unlike many African areas) has never allowed it to develop, in isolation and over an uninterrupted period of centuries, a type of animal suited to its own peculiar climatic pattern.

This difficulty of producing intermediate types has, to some extent at least, been solved in Africa. The two main climographs in *Figure 5.28* will serve to illustrate this point. The climograph for cattle of the northern sub-tropical coastal areas indicates a climate which does not involve extremes of either temperature or humidity. It abuts at its lower edge on to the typical climograph of temperate stock; its upper half crosses the critical 70°F line, but indicates neither excessive humidity nor aridity. The size, conformation and body covering of

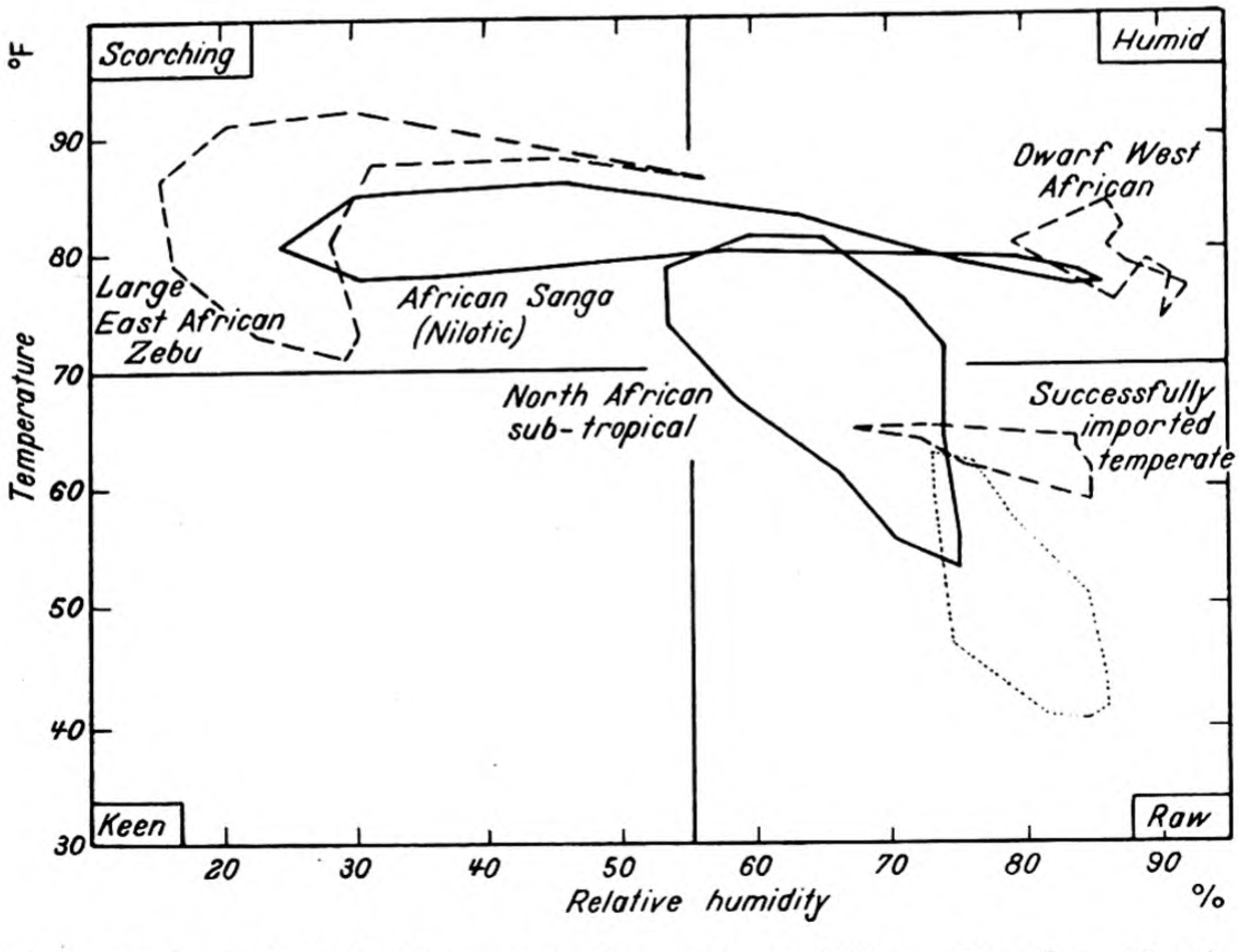

Figure 5.28. Typical climographs for cattle in Africa. *Details*:—North African sub-tropical (Cairo, Egypt); African sanga (Malakal, Anglo-Egyptian Sudan); large East African zebu (Khartoum, Anglo-Egyptian Sudan); dwarf West African (Ibadan, Nigeria); successfully imported temperate (Nairobi, Kenya). Climograph for London, England, is shown in fine dotted line.

the cattle represented by this climograph are, as already noted, intermediate in character to those of temperate and zebu stock. In contrast the climograph for the Nilotic Sanga type shows a uniformly high temperature but wide variations in humidity. Thus it is saved on the one hand from the dwarfing effect of a constant high humidity, and on the other from the need for the extensive fat reserves (and corresponding thoracic hump) of the true desert type. Both these intermediate types have been developed over centuries of breeding; both represent adaptations to an intermediate climate which, there is good reason to believe, have now reached equilibrium.

Apart from the climographs of these two intermediate types, *Figure 5.28* includes those for the African counterparts of the three extreme types already illustrated in *Figure 5.27*. The parallelism between type and climate in the two figures is exact. The large African zebu cattle (historically a direct descendant of imported Indian stock) show an almost identical climograph to the zebus inhabiting the Indian Plains; the climograph for the dwarfed stock of the West African coast is strictly comparable to that of the dwarfed animals of the hot-wet areas of the south-west coasts of India and of Ceylon; and the climograph for the only area in east or west Africa where European stock have been successfully introduced (*i.e.* the East African Highlands) coincides closely both with that of the parent European stock and with that of the hill station of Ceylon into which such stock have also been successfully introduced. In general therefore it may be claimed that the climographs for the African areas in *Figure 5.28* not only furnish information regarding the climatic conditions in areas inhabited by long established intermediate cattle types; they serve to confirm, by their close parallelism with the climographs of equivalent cattle types in Europe and Asia, their value as practical indices of homoclimatic environments.

Hythergraphs

Hythergraphs appear to have been first applied on any considerable scale by HUNTINGDON (1915) and subsequently by HUNTINGDON *et al* (1947) in their classic work in the field of economic geography. They have been used on a somewhat limited scale in ecological studies of domesticated animals, notably by Johnson (1924) and NICHOLS (1933). They are constructed in exactly the same manner as climographs, except that figures for mean monthly precipitation replace those for mean monthly humidity. In comparison with climographs their use as climatic indices for heat tolerance studies is limited, since rainfall can at best provide only a very rough guide of the atmospheric humidity. On the other hand they are unique in furnishing a combined indication of environmental temperature and of the probable nature, quantity and period of seasonal growth of the local vegetation.

For the reasons already stated their use will be illustrated here by reference to sheep. No attempt will, however, be made to discuss the detailed characteristics of the individual hythergraphs or to relate these to such important periods in the life cycle as the breeding and lambing seasons; full descriptions of their use for this purpose are given in the papers already cited by Johnson and Nichols. The intention is rather to indicate on a very broad basis the value of hythergraphs as indices of the markedly varying climatic environments of widely different types of stock. In *Figure 5.29* three hythergraphs have been included for typical temperate breeds, *i.e.* those for the northern mountain sheep, for the British Longwool and Down breeds, and for the original Spanish home of the fine-woolled Merino. Even between these three there are marked differences in the size and positions of the hythergraphs, indicating not only wide variations in the quantity and distribution of the rainfall but, with the Merino, a markedly hotter summer climate. But these are differences only in degree; in contrast the hythergraphs for the two fat-tailed types show strikingly the prolonged periods of complete drought which are the cause of the accumulation of their remarkable fat reserves. Moreover between these two types themselves there are differences in both temperature

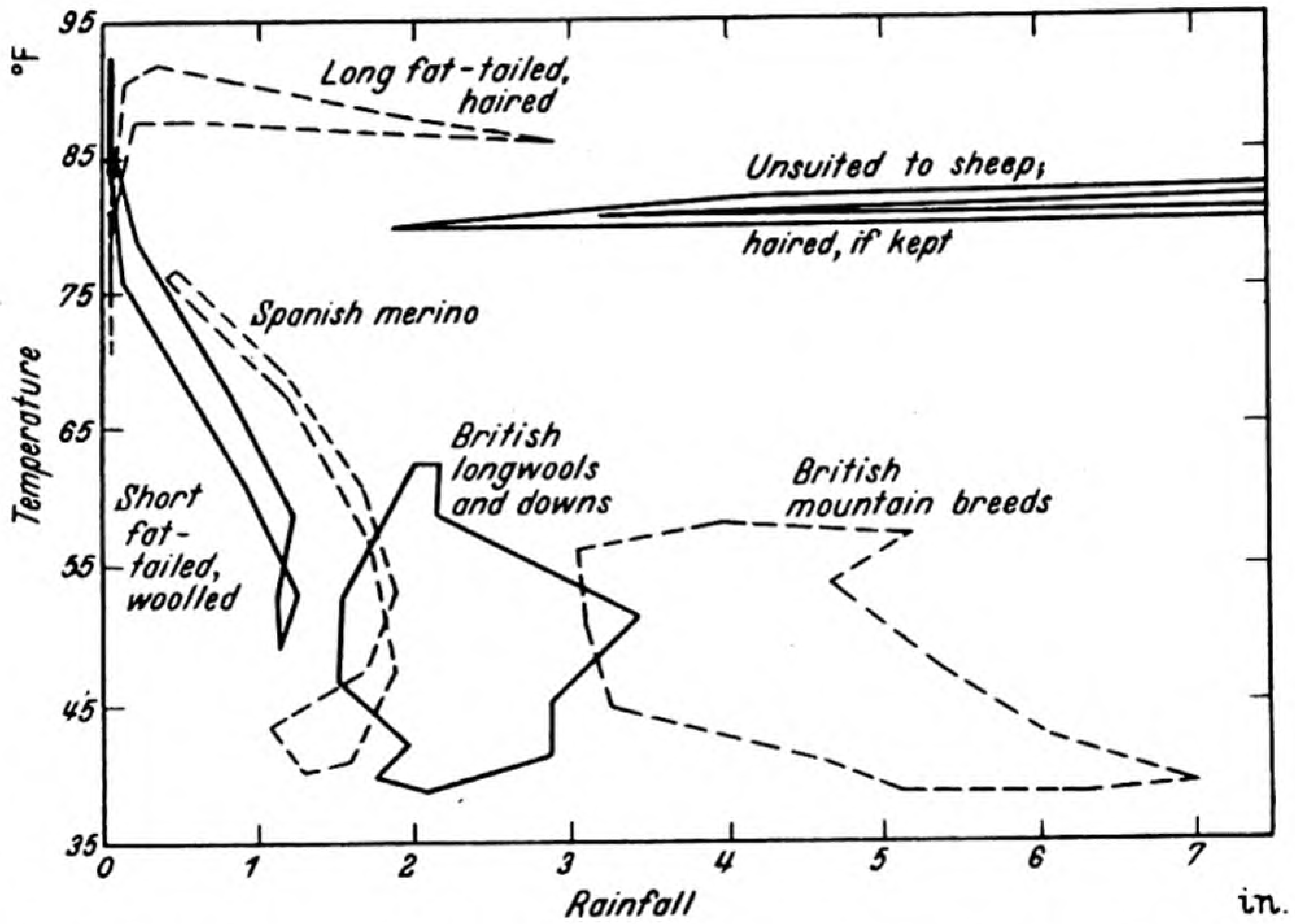

Figure 5.29. Typical hythergraphs for sheep in Europe and Asia. *Details*:—British mountain breeds and British Longwools and Downs (adapted from Nichols, 1933, and based on the Blackface and the Romney and Southdown respectively); Spanish merino (Madrid, Spain); short fat-tailed woolled (Baghdad, Iraq); long fat-tailed haired (Khartoum, Anglo-Egyptian Sudan); unsuited to sheep (Colombo, Ceylon).

range and rainfall incidence which can be correlated with their form and habits. Thus the short fat-tailed type of the northern deserts resembles its nearest neighbour, the Merino, both in its woolled coat and (as a result of the winter incidence of rainfall) in its close grazing habits; the haired coat of the long fat-tailed type of the southern deserts is, on the other hand, related to its uniformly hot environment, while the summer rains confer on it some of the characteristics of a browsing rather than of a grazing feeder. In marked contrast to both these hythergraphs is that of the sheep inhabiting hot-wet areas, where the rainfall is in fact too high to be included completely in the diagram. Such areas have, at most, only sparse populations of sheep, all of which (owing to the excessive heat) are haired and most of which are—for climatic as well as other reasons—of a scraggy and unproductive type.

It will be seen from these examples that while, from the physiological aspect of heat tolerance, the hythergraph is inevitably of less value than the climograph (though the inclusion of the environmental temperature goes some way to make good this deficiency), it nevertheless furnishes a climatic index which is readily interpreted and of great potential value to the practical stockman. Whether for this reason it will supersede the climograph as a convenient means of identifying homoclimatic areas, or whether both will be superseded by some more convenient index as a result of further study, remains an open question. In the section which follows full use will be made of both methods of assessment not only in examining past results, but in suggesting new lines of approach in regard to livestock improvement.

SOME RESULTS OF THE INTRODUCTION OF LIVESTOCK INTO NEW AREAS AND THEIR APPLICATION TO CURRENT IMPROVEMENT PROBLEMS

In the very early stages of animal domestication the practice of an invading or migrating people of advanced culture was to introduce their own livestock into the newly occupied territories, which seldom possessed any indigenous domesticated types. Probably the earliest recorded examples were the introduction of Asiatic stock into, and their migrations within, Europe and Africa, details of which have been described by Curson and Thornton (1936) for cattle, Bellini (1941) for sheep, and more generally in LYDEKKER's classical monographs (1912). So many centuries have passed since these early migrations and so sparse and controversial are the available data, that they can hardly be used to advantage in discussing present-day problems of the improvement of livestock by the introduction of exotic types, except to note the very long periods of time needed to produce fixed intermediate breeds such as those of Africa and the Middle East. On the other hand valuable lessons can be learnt from the relatively recent introductions of livestock into Australasia and America, as well as into certain colonial territories. The present discussion will be limited to sheep and cattle.

INTRODUCTION OF TEMPERATE STOCK INTO TEMPERATE AREAS

Turning first to sheep, introductions into Australasia form on the whole an encouraging story. In regard to New Zealand the climate is almost identical with that of Britain (compare *Figures 5.29* and *5.30*), from which most New Zealand sheep have been derived. Indeed recent figures show that more than four-fifths of all breeding rams are now either Romneys or Southdowns (Royal Commission, 1949), while these breeds or their crossbreds account for at least the same proportion of commercial stock (Dayus, 1953). Nevertheless even within the relatively narrow confines of New Zealand differences in the distribution of the temperate breeds occur. Thus the Romney has, in contrast to its very localized climatic distribution in Britain (*Figure 5.29*), developed certain characteristics in New Zealand, notably in conformation and wool covering, which have enabled it to serve as a substitute for the British mountain breeds, *i.e.* to thrive in areas with annual rainfall figures as high as 40 in. and at elevations of over 3,000 ft. (see hythergraph for North Island in *Figure 5.30*). Again, the Spanish Merino, originally imported into New Zealand from Australia, has failed to gain a foothold except in areas of higher temperature and lower rainfall in the South Island, the hythergraph

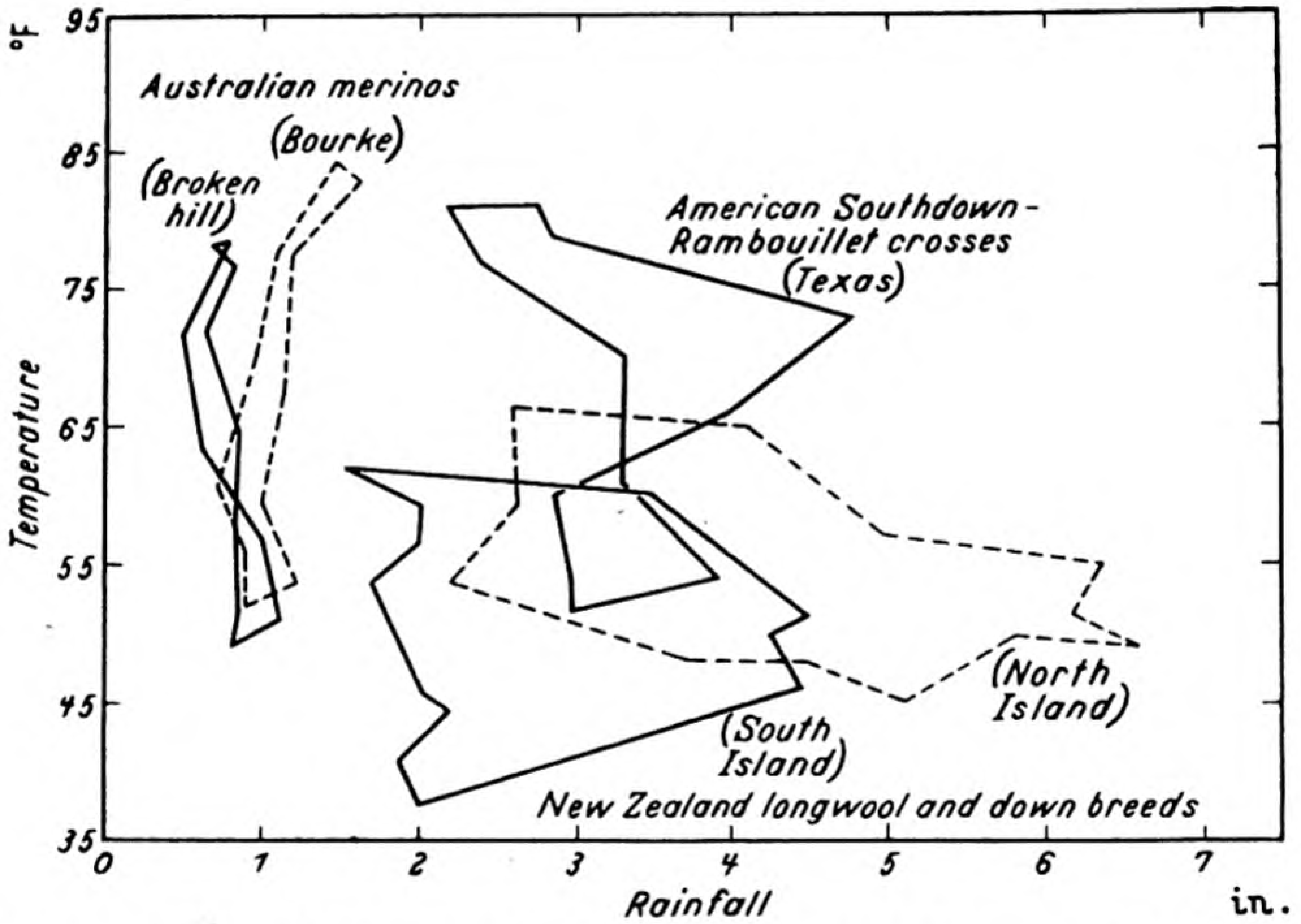

Figure 5.30. Hythergraphs for selected areas in Australasia and North America. *Details*:—New Zealand Longwool and Down breeds (composite for North and South Islands, adapted from Nichols, 1933); Australian Merinos (Bourke and Broken Hill, New South Wales); American Southdown-Rambouillet crosses (College Station, Texas).

for which lies somewhat closer to that typical of the Merino breed.

In regard to Australia, this general trend is paralleled. Breeds of British origin occupy (though in relatively smaller numbers) the cooler and wetter coastal belts, but it is the Merino which is the predominant breed in the vast warmer and drier areas. This breed, while requiring the better grazing of the rather wetter areas for stud stock, thrives with as low a rainfall as an inch a month and at temperatures up to and exceeding 75°F (TAYLOR, 1927). The hythergraphs of areas typical of commercial Merino flocks (*Figure 5.30*) show, in fact, almost exact coincidence with those of their Spanish progenitors (*Figure 5.29*). There are, however, still large tracts on the desert edge where conditions are too harsh even for the Merino, and an examination of the relevant hythergraph in *Figure 5.29* raises the interesting question whether the fat-tailed woolled sheep of the Middle East might not usefully be introduced into these marginal tracts—though the nomadic grazing typical of fat-tailed flocks has never been favoured in Australia. It is significant in this connexion to note not only the successful introduction of fat-tailed Karakuls into the lower rainfall areas of South Africa, but the widespread distribution there, in the more arid areas, of the fat-rumped and *haired* Blackhead Persian (NICHOLS, 1932, and South Africa, 1953).

In regard to North America, the same general pattern of distribution is again apparent. Thus Johnson (1924) has shown that the breeds of British origin thrive in the more northern homoclimatic areas of the United States, though he notes that, with the greater extremes of temperature, the better adapted Rambouillet (originally derived from the Spanish Merino) is to be preferred. He also notes a definite deterioration of the British breeds in the more southern warmer regions. His conclusions have been confirmed and extended by MILLER and MONGE (1946), who found, in the relatively hot Gulf areas, a poor level of production with the British breeds, a better record with Rambouillet and Delaine Merinos, but by far the best adaptation with Rambouillet-British crosses, whose hythergraph (*Figure 5.30*) confirms most strikingly their intermediate nature. The production of such crossbred types is, indeed, a common practice in American sheep breeding (HORLACHER and HAMMONDS, 1950) though such types are also subject to climatic limitations (WHITEHURST *et al*, 1947). As in South Africa, the fat-tailed Karakul has been introduced (chiefly for cross-breeding) into a number of climatically suited areas (KAMMLADE, 1947).

Turning to cattle, British stock have shown themselves well adapted to the more temperate areas of Australasia. In New Zealand, the climograph of which coincides closely with that of Britain (*Figure 5.31*), the earlier predominant breeds were the Dairy Shorthorn and the Jersey. Commercial requirements subsequently required a higher butter-fat percentage, and by a combination of pure-breeding and of grading-up, the proportion of Jersey and Jersey-crossbred stock was raised, within the brief period of fifteen years, from 30 to over 75 per cent (HAMILTON, 1944) and now stands at 85 per cent (Dayus, 1953), a remarkable example of a rapid and successful change of breed where animals within a homoclimatic area are used as sires. In Australia British cattle have also been introduced into the more temperate areas with complete success (Taylor, 1927). But the selection of breeds for the more northern hotter areas (the climates of which are in fact sub-tropical or even tropical) presents a very different problem (KELLEY, 1932 and 1943). This will be dealt with later.

The introduction of cattle into North America provides a very comparable picture to that of Australasia, though a more marked stratification in the distribution of the originally imported British breeds is found. Thus Davidson (1927) has shown that the large framed Holstein is the predominant dairy type of the northern States, the climograph for which, though showing more marked extremes (as does, for instance, Finland, to which British Ayrshires have been successfully exported (WILLIAMS and WRIGHT, 1932)), coincides in general with that of its British counterpart (*Figure 5.31*). In the more southern warmer States, however, animals of the smaller Channel Island breeds predominate. This difference in distribution has been attributed by Davidson to differences in size and hence in body surface and heat tolerance. On the other hand with beef cattle he found a similar stratification but no comparable gradient in body size; indeed he attributed the predominance of Shorthorns and Aberdeen Angus in the north and of Herefords in the south to the superior "rustling" qualities of the latter. In the light of the more recent work of BONSMA (1940, 1949b) it seems likely that here also differences in the mechanisms of heat tolerance (though of a different nature) may nevertheless have been the most important operative factor. In the extreme south of the United States, notably in the Gulf area, the climate is (as in the northern regions of Australia) sub-tropical or tropical in nature, to which no pure-bred temperate breed of cattle is really suited (RHOAD, 1938). This also will be dealt with later.

To summarize, it is clear that in general the transfer of stock from one temperate area to another can be accomplished satisfactorily; nevertheless if the imported breed is to be that best suited to its new environment, account must still be taken not only of purely local variations in the climate but of the more generalized climatic gradients within the importing country.

INTRODUCTION OF TROPICAL STOCK INTO TROPICAL AND SUB-TROPICAL AREAS

Just as the temperate breeds can be successfully introduced into homoclimatic temperate areas, so it seems clear (though available evidence is scanty) that tropical breeds can be no less successfully transferred for improvement purposes from one tropical area to another. Few recorded examples are available of the transfer of sheep, but cattle transfers have not been uncommon. Thus high yielding zebu stock have been exported from India to Ceylon (Wright, 1946), Cochin China and Cambodia (VILLEGAS, 1939) and Malaya (BUNTING and MARSH, 1934), both for pure breeding and for the straight grading-up of unproductive local stock. Judged from their climographs (*Figure 5.31*) this policy would seem to be equally applicable to

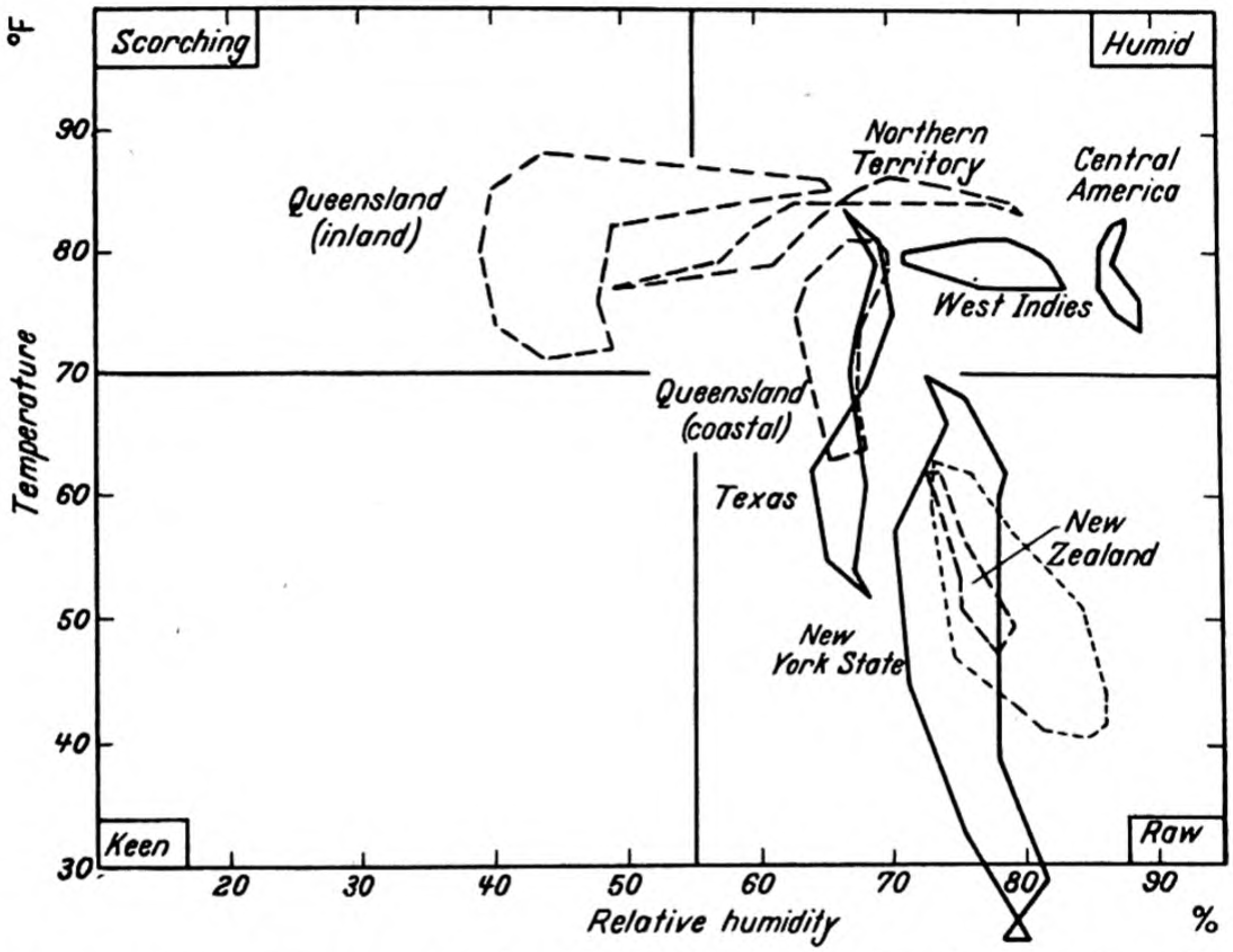

Figure 5.31. Climographs for selected areas in North America, the Caribbean and Australasia. *Details*:—New York State (Ithaca); Texas (San Antonio); West Indies (Port of Spain, Trinidad); Central America (Belize, Honduras); New Zealand (Wellington); Queensland–coastal (Rockhampton); Queensland–inland (Croydon, from Kelley's (1943) data); Northern Territory (Darwin). Climograph for London, England, is shown in fine dotted line.

the comparable hot-wet areas of the West Indies and central America; here, however, although zebus have been introduced, the purpose has in general been to use them for haphazard crossing with recently imported temperate breeds on an experimental basis (MAULE, 1953) rather than for consistent large scale stock improvement. It is interesting to note that, in regard to zebu introductions into Ceylon, recent experience (F.A.O., 1950b) has confirmed the conclusions regarding the relative suitability of certain individual Indian breeds which were forecast from the climographs published in Wright's original report.

But it is to the use of zebu stock for the production of intermediate cattle types suited to sub-tropical climates that the most ambitious programmes of cross-breeding have been directed. This is the objective at the King Ranch in Texas, where the deterioration of the temperate stock, mistakenly employed as the original basis for improvement in the hot environment of the southern coastal areas, is being mitigated by the introduction of zebu blood (KLEBERG, 1931; Rhoad, 1949). It is also the objective of the parallel experiments in the northern regions of Australia (KELLEY, 1932 and 1943), and of the development of the Ocampo cattle in Venezuela (F.A.O., 1950c).

In planning and implementing any such large scale improvement policies it is, however, necessary to take account of four considerations. First, it is essential to ensure that the earlier imported stock have not in fact already become fully acclimatized to their new environment. The powers of adaptation of the Romney in New Zealand have already been referred to. The beef cattle of the Argentine are largely derived from temperate European breeds, yet in many areas their constitution and productivity appear unimpaired in spite of the distinctly warmer climate. To make a drastic change in breeding practice might, in such circumstances, merely place the existing industry at risk. Second, it is no less essential to ensure that the imported zebu stock themselves possess the type of climatic tolerance required. Reference to *Figure 5.31* shows, for example, that in Texas the objective should be an animal comparable in heat tolerance to those of the sub-tropical coastal areas of North Africa (*Figure 5.28*), *i.e.* capable of tolerating, at moderate humidities, variations in temperature ranging from the temperate to the tropical. These conditions are seen to be identical (*Figure 5.31*) with those in the coastal areas of Northern Queensland, where Texas crossbred stock have now been introduced experimentally. But inland from the Queensland coast the climate changes; the range of temperature lies higher and the humidity is markedly reduced (*Figure 5.31*). Here the type of stock required should, on the basis of their climographs, resemble in climatic tolerance the large pure-bred zebus of India and Africa (*Figures 5.27* and *5.28*). Moving still further north and west to the coast of the Northern Territory, the climate shows a further change; the temperature is uniformly high and the humidity high though variable, conditions closely paralleled by the medium-sized pure-bred zebu inhabiting the coastal desert tracts of India (*Figure 5.27*). Moreover both the inland and the northern coastal areas of Australia are subject to periodic droughts, so that the existence of the fatty hump typical of the pure-bred zebu might well be advantageous. Thus it is clear that for each area there is a definite climatic pattern to which, for successful improvement by importations or cross-breeding, the imported breed itself must be adapted. Third, it is obviously advantageous that the imported animals should possess both size and conformation consistent with the purpose of improvement. Thus for both Texas and Australia animals of beef type are required; for these the pastoral areas of Africa might have been expected to provide a better source of heat tolerant stock than India, where cattle are bred predominantly for draught. Fourth, it must be recognized that improvement by cross-breeding is inevitably slow and fallible. The true-breeding intermediate cattle types of Africa and the Middle East have only been developed after centuries of selection and adaptation. The only possible short cut to an equal fixity of breeding is by the use of population sufficiently large to provide the fullest scope for both mutational change and selective improvement. Thus the evolution of the Santa Gertrudis type in Texas has involved a herd of 50,000 animals and is, in large measure, attributable to one or two exceptionally prepotent sires (Rhoad, 1949).

Provided these four considerations are taken fully into account it would seem that the judicious use of tropical stock should offer real scope for effecting livestock improvement (and particularly for redressing the errors of earlier temperate importations) in many of the sub-tropical areas of the New World.

INTRODUCTION OF TROPICAL AND SUB-TROPICAL STOCK INTO TEMPERATE AREAS

The foregoing discussion has been concerned with the introduction of stock into areas to which they are already climatically adapted, *i.e.* into *homoclimatic* areas. The reverse, their introduction into *heteroclimatic* areas, raises new issues which it is clearly necessary to examine in some detail.

It is rare for tropical and sub-tropical stock to be introduced into temperate areas for improvement purposes, since it is in temperate stock that high levels of productivity have usually been developed. There are, however, a few exceptions to this rule. The most notable is the horse where (as already noted) the more northern countries have imported southern breeds (notably the Arab), primarily to improve the speed of their slower and heavier indigenous types. A second is the goat, where in particular the long-eared Nubian breed has been introduced to improve the productivity of our temperate stock. A third is the ass, the distribution of which is, however, largely confined to the warmer areas of the temperate zones and which elsewhere (notably in the United States) is used almost solely for the breeding of mules. All three of these classes of livestock are tropical or sub-tropical in their origin as well as in their body characteristics, and the question naturally arises whether, in course of time, they will tend to degenerate under temperate conditions. It appears, however, that the introduction of heat tolerant types into colder environments does not in practice involve any serious hazard. This is partly because physiological adaptations to low temperature seem better developed (Findlay, 1950), partly because artificial means of protection against extremes of cold are easier and cheaper to devise than against extremes of heat, and partly because the conditions of feeding and management in the more highly developed settled areas of the temperate zones are on a far higher plane than is possible in the more primitively settled or predominantly pastoral areas of the tropics.

INTRODUCTION OF TEMPERATE STOCK INTO TROPICAL AND SUB-TROPICAL AREAS

On the other hand there is clear evidence of very real hazards when temperate stock, usually of high productive capacity, are imported into tropical or sub-tropical areas as a basis for livestock improvement. This is true whether such stock are used for pure or cross-breeding—the latter practice having been frequently adopted in a wide variety of areas, invariably with unsatisfactory results.

Turning first to cattle, Maule (1953) has reviewed much of the available evidence, particularly regarding the introduction of British dairy breeds into tropical areas. Even in regard to productivity it appears that after the first crossbred generation (which enjoys hybrid vigour) and possibly the second, milk yields tend to fall to or below their original levels. But even more striking are Maule's comments on the condition of the crossbreds continuously backcrossed to temperate stock. Thus in the West Indies repeated backcrossing to Friesians resulted in an increase in discards to a level of nearly 60 per cent; in the Philippines (with a comparably hot-wet climate) mortality among young stock rose to nearly 50 per cent with continuous backcrossing to Ayrshires; in Egypt backcrossing to Shorthorns resulted in stock which were inferior in growth rate, disease resistance and adaptability, and in Jamaica backcrossing to Jerseys was reported as being successful up to a point but that " some reinfusion of zebu blood from time to time was found necessary ". WRIGHT (1936) has reported that in India repeated backcrossing to imported temperate breeds resulted in a deterioration in physique and in high mortality, particularly among calves. Villegas (1939) similarly reported that Cochin China, Cambodia and Malaya all failed to maintain dairy cattle from temperate countries except at one hill station, while FRENCH (1941) commented on the failure of both pure and high grade European cattle to withstand the hot conditions in East Africa. In regard to beef cattle BISSCHOP (1938) noted regressive changes in animals backcrossed to British beef or dual purpose breeds, while MANRESA (1934) stated in a review of a quarter of a century's work in the Philippines that " as the percentage of Hereford blood increased, the progeny reverted to the pure Hereford parents in constitutional weakness ". Further examples of the unfavourable results of introducing temperate breeds, both of dairy and beef cattle, into tropical territories have been cited at a recent F.A.O. conference (1950) and by Faulkner and Brown (1953).

Comparable information regarding the introduction of other classes of temperate stock into tropical areas is scanty. In India crossbred sheep with a high proportion of Merino blood showed a high mortality rate; out of over 1,000 sheep issued in a single district none survived for more than a few months (NANDA, 1947). In Iraq it was found that Merinos failed to stand up to the desert conditions (WRIGHT, 1945). Moreover where such sheep did survive a ' break ' was apt to occur in the staple as a result of the hot season (IRAQ, 1930). In Palestine imported Merinos showed a high mortality; the sheep suffered from heat and all the lambs died within the first year (HIRSCH, 1933). Similarly attempts to introduce Scottish Blackface, Dorset Horn and Cheviot-Dorset rams proved unsuccessful; some died, others suffered greatly from the heat. Crossbred lambs remained stunted, lost condition and succumbed to disease (SMITH, 1936). In regard to horses, perhaps the most striking comment is that in the Sudan " the chance of survival diminishes in inverse ratio to the amount of imported blood " (SUDAN, 1942).

These examples are sufficient to indicate the danger of introducing temperate stock into tropical and sub-tropical areas; and while susceptibility to disease, tick infestation, intestinal parasites and the like must clearly have played their part (though these themselves can hardly be dissociated from the ecological environment), there seems little doubt but that the primary cause of the high mortality and morbidity (and indeed of the low productivity) was lack of adequate tolerance to the heteroclimatic environment. Moreover these examples are not exceptional; indeed, a search of the literature has failed to reveal a single instance of an adequately controlled long-term breeding trial where, sooner or later, either the introduced or backcrossed stock has not degenerated or it has not had to be reinvigorated (at the cost of the abandonment of any consistent breeding policy) by the reintroduction of the indigenous or of some similarly suited homoclimatic breed.

Where, then, lies the solution to the problem of livestock improvement in these hotter or more humid areas? First, clearly, in the acquisition of increased knowledge (on lines which have been fully described in the recent review by Findlay, 1950) of the climatic factors which affect heat tolerance. Second, in a wider recognition of the importance of climatic assessment (based, wherever possible, on uniform methods of field study such as those detailed by LEE, 1953) as a rational basis for stock selection and introduction. And third, in raising the productivity of indigenous stock over the widest possible ranges of both climate and environment. Only when such a series of reservoirs of potentially productive stock have been established (and this is the objective of a number of current livestock improvement schemes (F.A.O., 1950)) will it be possible, either in introducing new breeds or in improving the old, to conform more closely to the ecological principles which have formed the subject of this chapter.

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CHAPTER 6

ENVIRONMENTAL PHYSIOLOGY OF FARM MAMMALS

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WITHIN recent years much has been published on the environmental physiology of farm animals, and comprehensive reviews have been written by BRODY (1945, 1948), LEE and PHILLIPS (1948) and FINDLAY (1950, 1954). The fundamental problem with which this literature deals is that of heat regulation in farm mammals, principally cattle. The subject has a wide economic significance and involves many variables and branches of science, encroaching as it does on the territory of the physiologist, animal husbandryman, engineer, architect, meteorologist and biophysicist. Man has for long been able to modify his own private climate by the use of clothes and by more or less elaborate air-conditioning methods. His efficiency has been known to be intimately bound up with the control of his thermal environment. It is only recently, with the recognition of the tropics as main sources of world food supplies in the future and the need for increasing the efficiency of farming in temperate climates, that interest in the thermal surroundings of farm animals has been evoked.

Cattle are now transported in large numbers from temperate to tropical zones and from semi-tropical zones to zones where extremely cold conditions may prevail. Productivity in the tropics is low and many factors play their part in maintaining this low level. Breeding, nutrition and management are all involved. The indirect effect of climate on crop production sets a very low standard for the nutrition of animals in some parts of the tropics, and in many areas it appears virtually impossible to raise this standard. Better management could increase production, but management is bound up with complex sociological and economic considerations. Breeding has been the expedient most frequently used to improve productivity in the tropics, since it has been assumed that where local indigenous livestock were of poor productive capacity production could be improved either by importing better breeds from overseas and establishing herds of these as pure bred stock or by crossing them with the native cattle. This latter course has gradually focused attention on the direct effects of climate on cattle and so on the nature of temperature regulation in cattle.

It has come to be recognized that in temperate regions ventilating standards for farm animal shelters have been either neglected or formulated on a purely arbitrary and non-scientific basis (FINDLAY, 1948). Animal husbandrymen have now realized that there are specific thermal environments for optimal production and that draughts, air temperature, humidity and rate of air movement can profoundly affect animal production. This seeking for physiological standards of ventilation has also been a driving force in research on the climatic physiology of farm animals.

The world-wide interest that now exists in the subject can readily be seen from F.A.O. publications by PHILLIPS (1948, 1950a, b) which deal with the improvement of livestock under tropical conditions and the breeding of livestock adapted to unfavourable environments.

The purpose of this chapter is to illustrate from the work of the last 15 years or so the advances that have been made in knowledge of the environmental physiology of farm animals. Since little work of importance has been published on the environmental physiology of farm animals other than cattle, the chapter deals principally with the bovine animal but many of the findings discussed are applicable to sheep and pigs.

NATURE OF TEMPERATURE REGULATION

All farm animals—sheep, cattle and pigs—are homeotherms. They attempt to maintain their body temperatures within the range most suitable for optimal biological activity. In order to do this they must maintain a thermal balance between the heat they produce or gain from their environment and the heat they lose to their environment. A diagram showing the main routes of heat production and gain and those of heat loss is given in *Figure 6.1*. The diagram is for cattle but with little modification it applies to other farm mammals. All the heat produced must eventually be dissipated by the four channels of radiation, conduction, convection and evaporation. Ingestion of food and the utilization of body reserves results in heat being produced for maintaining essential body processes such as body temperature, cardio-respiratory activities and muscle tone. Productive processes such as milk production involve increased heat production, *e.g.*, a non-lactating, resting dairy cow might produce heat at the rate of about 12,000 Cal./day, but the same cow yielding 4 gallons of milk per day might produce twice this amount. The heat of fermentation in the rumen also adds to the heat produced.

Heat production may be increased by several other factors, *e.g.*, by the heat increment of feeding as illustrated in *Figure 6.2* from data given by BRODY (1948). The state of activity and posture of the animal also influences its heat production, *e.g.*, in the fasting steer

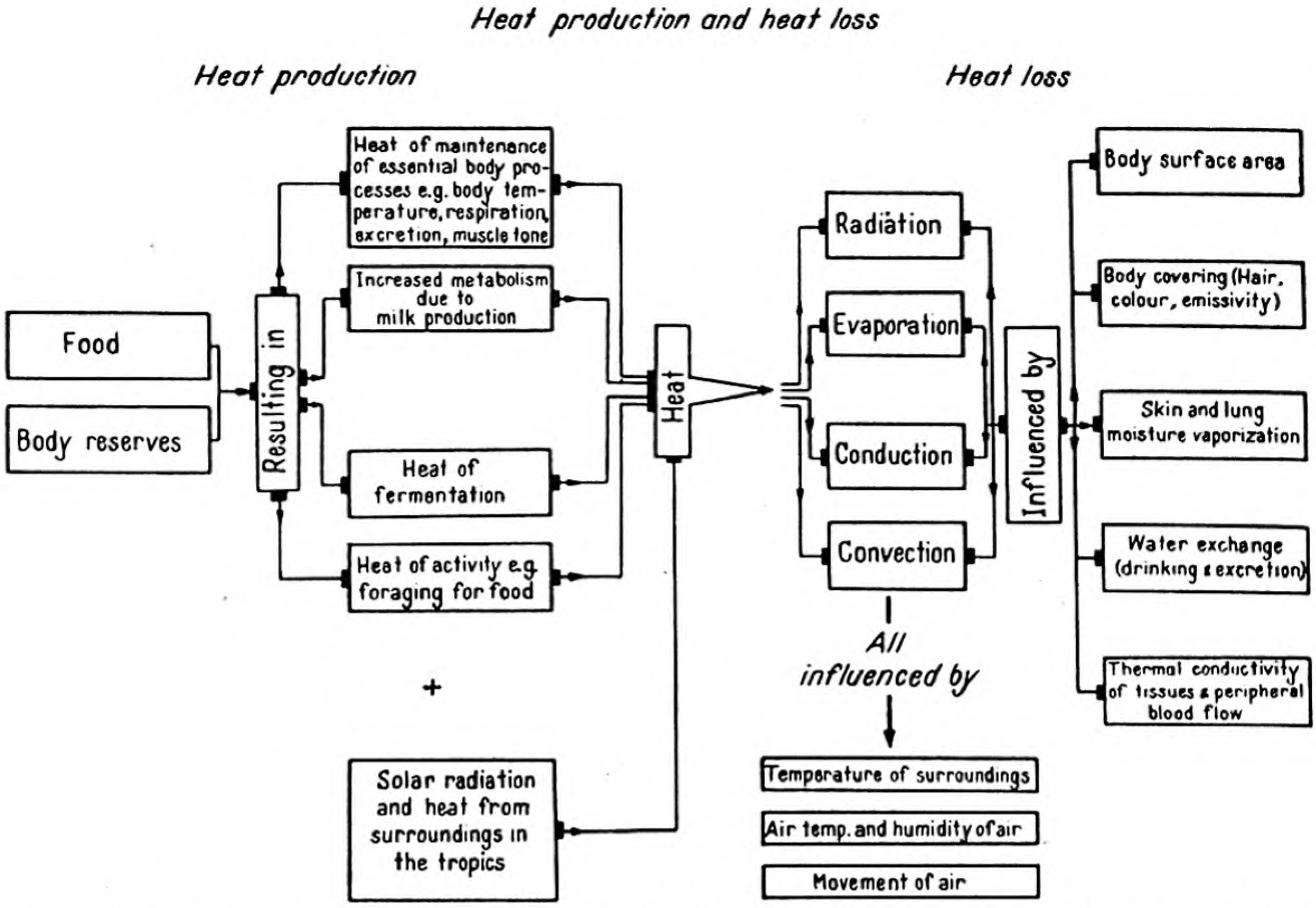

Heat production and heat loss
Heat production
Heat loss
Food
Body reserves
Resulting in
Heat of maintenance of essential body processes e.g. body temperature, respiration, excretion, muscle tone
Increased metabolism due to milk production
Heat of fermentation
Heat of activity e.g. foraging for food
+
Solar radiation and heat from surroundings in the tropics
Heat
Radiation
Evaporation
Conduction
Convection
All influenced by
Temperature of surroundings
Air temp. and humidity of air
Movement of air
Influenced by
Body surface area
Body covering (Hair, colour, emissivity)
Skin and lung moisture vaporization
Water exchange (drinking & excretion)
Thermal conductivity of tissues & peripheral blood flow

Figure 6.1. Diagram showing the principal methods by which heat is produced, gained and lost in cattle. In the tropics solar radiation and high temperature of the surroundings can add considerably to the heat load. The term 'Heat of Activity' is intended to include all heat produced as a result of muscular activity (from Findlay, 1950, by courtesy *Bull. Hannah Dairy Res. Inst.*).

or cow the energy expended in standing is about 9 per cent greater than it is when the animal is lying down, and the energy required in getting up or down may amount to about 12 Cals. per 100 lb. body-weight. If the animal is moving about, still further increases may occur due to the extra muscular activity. Thus, when a cow walks a mile the energy required additional to that for maintenance and standing amounts to about 330 Cal./1,000 lb. liveweight, while a 50 kg. sheep may expend an extra 40 Cal./hr. when walking at 2 m.p.h.

In cold conditions the need is to obtain and conserve heat and in warm conditions to dissipate it. Thus in the former condition heat production is increased by eating more, by shivering (which is a form of muscular activity), or if food is insufficient by using body reserves to supply the extra heat required. Nevertheless the means whereby an animal can vary its heat production are very limited compared with the means at its disposal for conserving or eliminating heat. A deeper insight into temperature regulation is more likely to be obtained by the study of heat loss mechanisms than by studying the effects of environment on heat production processes. It is in fact with heat loss mechanisms that most recent work both in farm animals and in man has been mainly concerned.

PHYSICAL PATHWAYS OF HEAT LOSS

Animals lose heat by radiation, convection, conduction and evaporation.

Radiation Loss

Heat loss by radiation from the animal body is given by the equation:

$$H_r = A\rho(e_1 T_1^4 - e_2 T_2^4)$$

in which A is the effective or profile surface area of the animal, T_1 is the absolute temperature of the animal's surface and T_2 the absolute temperature of the surrounding surfaces, ρ is the dimensional constant in the Stefan-Boltzmann Law which states that the emissive power is proportional to the fourth power of the absolute temperature; e_1 is the emissivity, virtually 0·95 for animal or human skin, and e_2 the emissivity of the surroundings. Radiation loss is therefore related to the surface area of the animal, but the amount lost in this way will, of course, depend on the posture of the animal, *e.g.* a 'huddled' animal will lose less heat by radiation to its surroundings than when it is spread-eagled. It is also related to the temperature of the animal's skin and the temperature of its surroundings and to the emissivity of the animal's skin, *i.e.* how nearly its skin approximates to a perfect absorber and emitter of heat. The insight gained into radiation loss from farm animals by study of their skin characteristics is dealt with later.

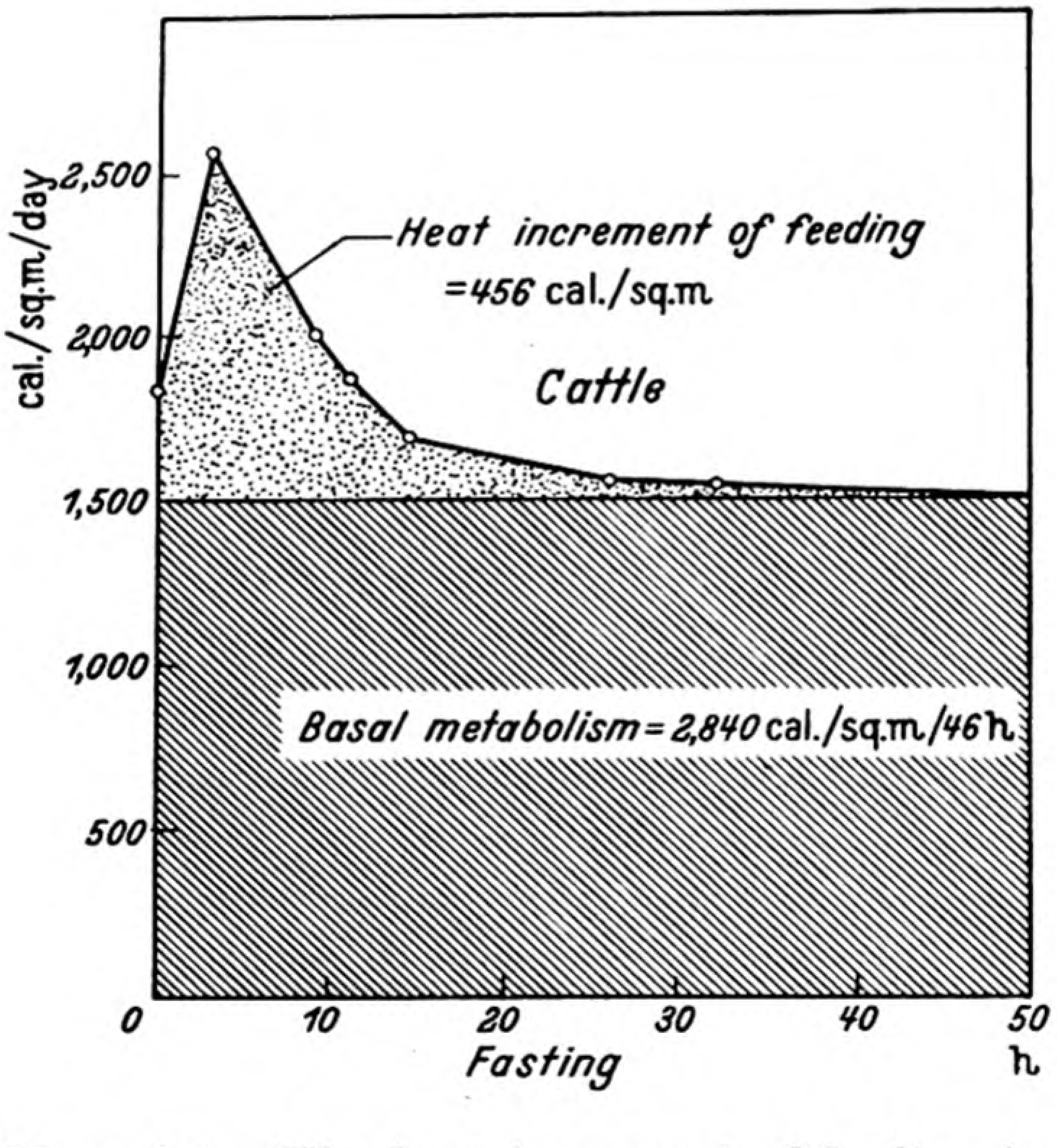


Figure 6.2. The heat increment of feeding in cattle (adapted from Brody, 1945).

Convective Loss

The rate of heat dissipation by convection is also proportional to the surface area of the animal as indicated in the following equation :

$$C = kA\sqrt{v}\,(t_1 - t_2)$$

where C is the convection rate, A the surface area, v the velocity of the air and t_1 and t_2 are the temperatures of the body surface and the environment respectively; k is the convection conductance. Convective loss is thus seen to be affected by the surface area of the animal and consequently it will vary with the posture of the animal. It will also be affected by the velocity of the air moving past the animal's surface and by the temperature of the animal's surface and of the ambient air.

Conductive Loss

An animal loses heat by physical contact with surrounding surfaces and the magnitude of this loss will depend on the thermal conductivities of the contacting surfaces, their areas and their temperatures. The relationships, for example, for a pig lying on a concrete floor are exceedingly complex and have not been formulated, since in this and similar instances the time for which the animal is in contact with the surface conducting heat to or from it must also be considered.

Evaporative Loss

Potentially the evaporation of water is the most important means of dissipating heat. At 91·5°F., 1 g. of water on evaporation carries with it approximately 580 cal. Evaporation of water from the skin and respiratory surfaces accounts for much of the heat lost by an animal. Evaporation of water from the skin as a heat loss mechanism will depend on the temperature of the skin, the covering of the skin, the humidity of the surrounding air and the water available for evaporation. Where the skin has a hair covering, water vapour may be entrapped and a layer of high humidity be maintained over the surface of the animal. The hair will also reduce the movement of the air which is in contact with the skin. Heat lost by vaporization from the lungs will be governed by the respiratory minute volume and the humidity of the inspired and expired air.

This brief discussion of the physical pathways of heat loss is sketchy, and it is designedly so in view of the fact that little is known of the physical constants involved for farm animals. More detailed treatment of the subject will be found in publications by GAGGE (1941), WINSLOW (1941), HARDY (1949) and HERRINGTON (1949). These papers give most of the leading references on the subject.

From what has been written it will be seen that temperature regulation in farm mammals will be reflected in their behaviour in the field, *e.g.* in their grazing habits; in the behaviour of their rectal temperature both as an indicator of thermal balance and in the maintenance of a suitable temperature gradient between the sources of heat production and the skin; in the role played by their skin and skin covering and their respiratory activities; in their cardiac activities as an index of peripheral blood flow and hence conduction of heat to the surface, and in their degree of productivity. It will be shown that the main mechanisms used by cattle, and apparently by sheep and pigs, to maintain a thermal balance under conditions of thermal stress, are polypnoea whereby heat loss is increased by increasing the amount of vaporization of moisture from the respiratory passages, transudation of moisture through the skin and the reduction of heat production by voluntary anorexia. It will also be shown that such behavioural mechanisms as increasing the amount of water drunk, seeking shade and diminishing muscular activity are important.

For temperature regulation in very cold conditions farm animals tend to increase their heat production by increasing the amount of food eaten. They also tend to increase their degree of insulation by laying down increased amounts of fat sub-dermally and by developing longer hair in winter. They increase heat production by shivering and conserve heat by huddling together.

Before discussing the results of recent research on the behaviour of farm mammals in different thermal environments present knowledge on the central control of temperature will be considered.

THE CENTRAL NERVOUS CONTROL OF TEMPERATURE

Virtually nothing is known of the central control of temperature in farm mammals, but much has been done with man and laboratory animals, though even for them the knowledge obtained is far from complete.

Present trends of thought are agreed that the centres for the control of body temperature are situated in the hypothalamus with subsidiary centres higher in the cerebral cortex capable of modifying reactions, and lower in the medulla and spinal cord which have an integrative function. In view of the complex neuro-endocrinological associations of the hypothalamus the reader should beware of facile over-simplification in regard to the assignment of function in this area.

The theory of thermal control still widely accepted is that of MEYER (1913) *i.e.* the ‘dual centre’ theory, which postulates that there are two centres in the hypothalamus associated with overheating and with overcooling respectively. This central thermoregulatory apparatus contains cells which are sensitive to changes in blood temperature. Presently held theories demand that this thermostat-like mechanism should be responsive to the temperature of the blood in the vicinity of its sensitive cells. This means in effect that it is the temperature of the centres in the hypothalamus that has to be regulated.

Acting as an additional regulator to the main centre is the peripheral mechanism of heat and cold sensory endings in the skin, and the vasomotor, sweating and shivering activities which they control.

GRANT (1951) has stated in an admirable review, that even fragmentary understanding of hypothalamic function in temperature control will not be achieved until adequate techniques have been developed for the recording of brain stem potentials, so that the effect of central and peripheral thermal stimuli on the efferent discharge of hypothalamic neurons may be studied. The position with regard to the absolute nature of the thermostat-like mechanisms will probably be clarified only when techniques for the implantation of thermocouples in the circle of Willis become more highly developed and more widely used than at present.

Adequate and stimulating reviews of present knowledge on the central control of temperature, derived mainly from studies on man and laboratory animals have been published by BAZETT (1949), HARDY (1950) and GRANT (1951). The operating characteristics of the human thermoregulatory mechanism have been conjectured by BURTON (1941) and BARBOUR (1941) has dealt with the development of homeothermy in mammals. Among the older literature on temperature regulation in man and laboratory animals the reviews of BAZETT (1927), SUNDSTROEM (1927), DIGHTON (1933), and DU BOIS (1941) will be found useful.

HEAT REGULATION IN FARM MAMMALS AS REFLECTED IN THEIR BEHAVIOUR AND PHYSIOLOGICAL REACTION TO DIFFERENT THERMAL ENVIRONMENTS

Recent studies on the effect of different thermal environments on the behaviour and physiological reactions of farm animals have taken two forms. Much information has been collected by observing the grazing habits of animals in the field and by studying their respiration rates and rectal temperatures under different outdoor thermal environments. Much of this work has suffered from the uncontrolled nature of the experiments but it has nevertheless produced much information of value in assessing the reaction of farm mammals to thermal environment. Most of these studies have dealt with high temperatures in tropical or semi-tropical areas, but more recently, intensive work has been done in controlled-temperature laboratories or psychrometric rooms on the reactions of cattle to high thermal environments and also to temperatures down to 0°F. Such rooms and the experiments conducted in them have been described by BRODY (1948), FINDLAY (1950, 1953) and BEAKLEY (1954). A large psychrometric room of this type is shown in *Figure 6.3*, and the interior of a small one-animal chamber together with its associated measuring or observation room is shown in *Figure 6.4*. Experiments in the large psychrometric room have taken the form of exposing groups of cattle of various breeds to temperatures from 0° to 105°F. and comparing their physiological reactions as reflected in their milk yield, feeding habits,

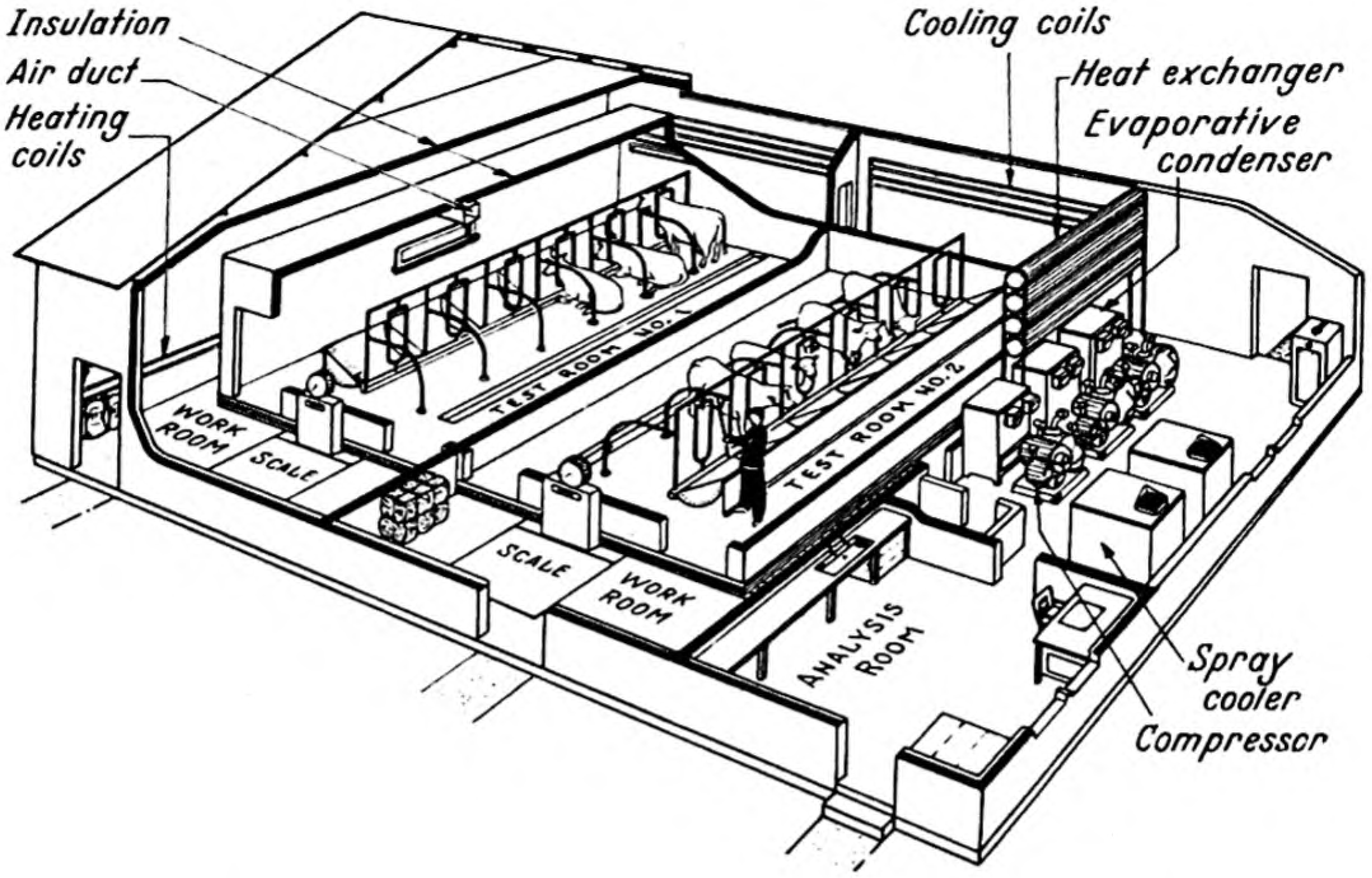

Insulation
Air duct
Heating coils
Cooling coils
Heat exchanger
Evaporative condenser
WORK ROOM
SCALE
TEST ROOM NO. 1
TEST ROOM NO. 2
SCALE
WORK ROOM
ANALYSIS ROOM
Spray cooler
Compressor

Figure 6.3. The psychroenergetics laboratory for cattle at the University of Missouri, U.S.A. (from Brody, 1948, by courtesy *Res. Bull. Mo. agric. Exp. Sta.*).

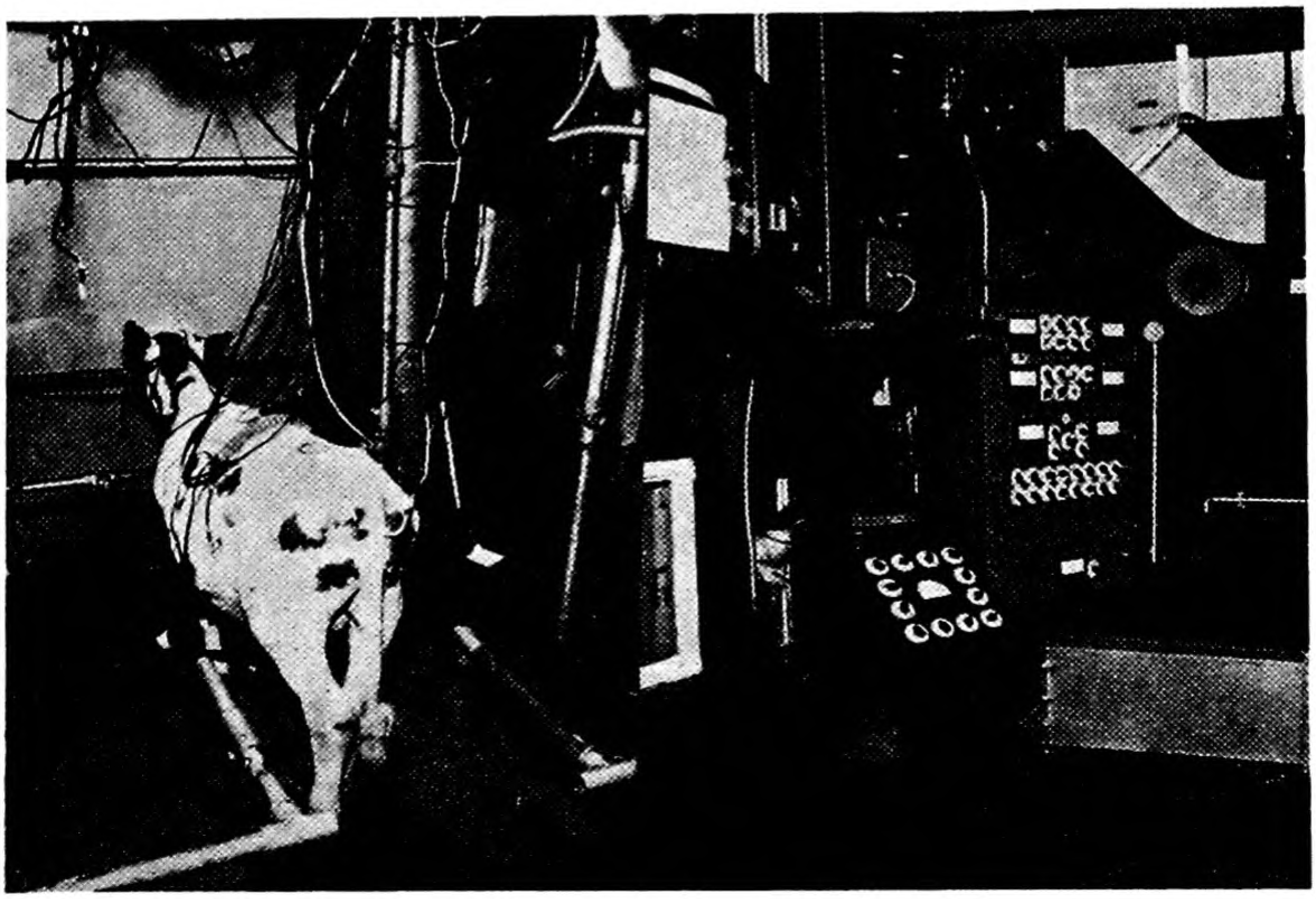


Figure 6. 4. A psychrometric room and observation room for environmental studies on cattle at the Hannah Institute.

blood chemistry, cardiorespiratory behaviour, water exchange, body temperature reaction, insensible weight loss and skin temperatures with those of similar groups held under controlled conditions of around 50°F. In the smaller type of room single animals (calves) have been intensively studied to determine the effect of temperature, humidity and time of exposure on physiological reaction as measured by cardiorespiratory behaviour and rectal and skin temperature reactions.

GRAZING HABITS

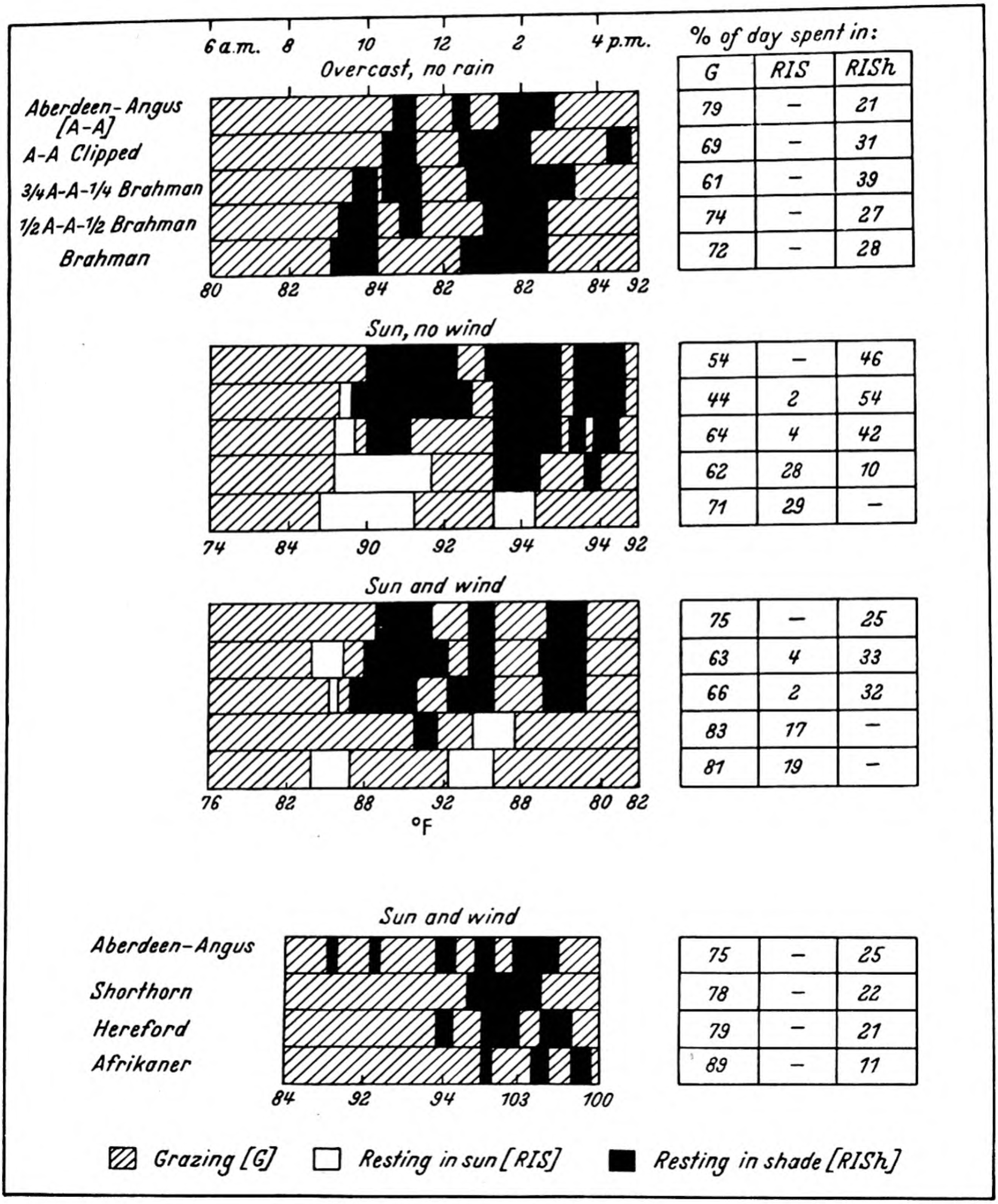
In high thermal environments cattle and other farm animals will tend to reduce their heat production by voluntary anorexia. This reduction in food intake as a means of reducing the heat load is consequently reflected in their grazing habits, when by grazing less they reduce both their food intake and the muscular activity involved in foraging for food.

There have been many studies in recent years relating grazing habits to environmental temperature; they have been of value in describing the resistance of various types of cattle to heat stress and in emphasizing the need for ameliorative measures in the form of shade and shelters.

A diagram (*Figure 6.5*) compiled by FINDLAY (1950) from data given in the literature shows the grazing behaviour of a variety of breeds and cross-breeds of cattle exposed to different weather conditions. It is clear from this figure that under hot sunny conditions, the grazing time of cattle is related to the proportion of tropical blood present and that clipping of the coat slightly alleviates the heat burden on the animals as judged by their grazing time. It will also be seen that the grazing time of the pure temperate breed, the Aberdeen-Angus, in overcast weather conditions was much greater than in sunny conditions with no wind. Wind tended to alleviate the effects of high temperature for all the animals.

Other workers (SEATH and MILLER, 1946) observed the grazing habits of Jersey and Holstein cattle at air temperatures from 60° to 90°F and found that animals sought the shade at an air temperature of about 80°F., when their body temperatures reached 102·4°F. which was about 0·7°F. above their normal body temperature. On days when the shade temperature was 85°F. the animals spent only 11 per cent of their time grazing, though at night when the air temperature was 81°F., 37 per cent of their time was spent grazing. This demonstrates clearly the effect of direct solar radiation in adding to the heat burden of the animals.

This effect of solar radiation on the grazing habits of cattle is important in indicating the need for providing good night pasture for animals which have to withstand daytime temperatures of 80°F. and beyond, a point recently recognized by PAYNE, LAING and RAIVOKA (1951) who observed the grazing habits of Friesian cows in Fiji. They showed that the cows grazed mainly at night (67 per cent of their total grazing time) and spent only 10 per cent of the nocturnal period in lying down as against 66 per cent of the daytime period.



% of day spent in:

G	RIS	RISh
79	–	21
69	–	31
61	–	39
74	–	27
72	–	28
54	–	46
44	2	54
64	4	42
62	28	10
71	29	–
75	–	25
63	4	33
66	2	32
83	17	–
81	19	–
75	–	25
78	–	22
79	–	21
89	–	11

Figure 6.5. A comparison of the grazing habits of cattle under different climatic conditions (from Findlay, 1950, by courtesy *Bull. Hannah Dairy Res. Inst.*).

The efficiency of heat disposal and the effect of environmental conditions on the physiological behaviour of cattle is therefore reflected in their grazing habits and it is apparent that there are very striking differences in the heat tolerance of various breeds and especially between temperate and tropical breeds as judged by grazing behaviour. Even within temperate breeds differences in grazing habits suggest that there are differences in heat tolerance. These results confirm the views of BROBECK (1948a, b), and MILLS and OGLE (1939) that the control of food intake is one of the natural mechanisms of heat regulation.

As a direct outcome of grazing behaviour studies many workers have investigated ameliorative measures that may be taken to increase the food intake of cattle exposed to hot conditions. Water sprinkling, shelter and increased air movement have been used either singly or in combination, as described by SEATH and MILLER (1947, 1948a, b). They showed that after 2 hours in an ambient air temperature of 88°F. the rectal temperature of Jersey cows was 104°F. Sprinkling them with water at 85°F. reduced the rectal temperature by 0·9°F.; sprinkling with water plus air movement reduced the rectal temperature by a further 0·3°F. while sprinkling with water in the shade plus air movement reduced the rectal temperature by 1·8°F. In other experiments FRYE, MILLER and BURCH (1950) showed that in air temperatures of 89°F. cows of European breeds with access to sprinklers grazed 42 per cent of their time while those with access to shade only, grazed but 34 per cent of their time.

Suitable types of shelters for use in the field under tropical conditions have been very fully investigated by KELLY *et al* (1950; 1951), who showed that the highest rate of liveweight gains were made by a group of cattle under a desert cooler which consisted of a three sided shelter open to the north with an upper roof of aluminium, a sub-roof of three layers of old hay and with an evaporative cooler under the roof at the south end of the shelter. Given a free choice between a galvanized-iron roof shelter, a louvred shelter and a hay-covered shelter with an iron sub-roof and no cooler, the animals chose the last of these and never chose the galvanized-iron roofed shelter.

MINETT (1947) has investigated the effect of artificial showers, natural rain and wallowing on the body temperatures of water buffaloes, zebu cattle, small hill cattle and sheep. A diagram, *Figure 6.6*, from data given by this worker, shows the effect of natural rain under air temperature conditions of about 59°F. on the rectal temperature of sheep and of small hill bulls exposed at Mukteswar during the monsoon period. Decreases of 1·6–3·8°F. in rectal temperature of cattle and of 1·4–2·7°F. in the rectal temperature of sheep were observed.

RECTAL TEMPERATURE

A great many observations have been made on the reaction of the rectal temperature of cattle to different thermal environments both in the field and in the laboratory. A few similar observations have been made on sheep and pigs. **Findlay** (1950) has reviewed work dealing with the effects of environmental temperature on the body temperature of cattle. The normal body temperature of cattle of temperate breed is usually accepted as 101°F. and an abnormally high temperature may indicate inefficient thermolysis. Results from field work indicate that the body temperature of temperate cattle increases with increasing air temperatures above 50°F. Laboratory studies on Jersey cattle (**Rieck** and **Lee**, 1948a, b) have shown that both cows and calves of that breed increase their rectal temperatures with rising air temperatures and have abnormal body temperatures at 85°F. air temperature. More recent psychrometric room studies (**Kibler** and **Brody**, 1949; 1950a; 1951; **Kibler**, **Brody** and **Worstell**, 1949) have shown that the rectal temperature of Holstein cows and Jersey cows increased at air temperatures from 70 to 100°F., the rectal temperatures of Holstein cows generally showing the greater rises. At 105°F. air temperature the rectal temperature was 108°F. in the Holsteins and in one of the Jerseys.

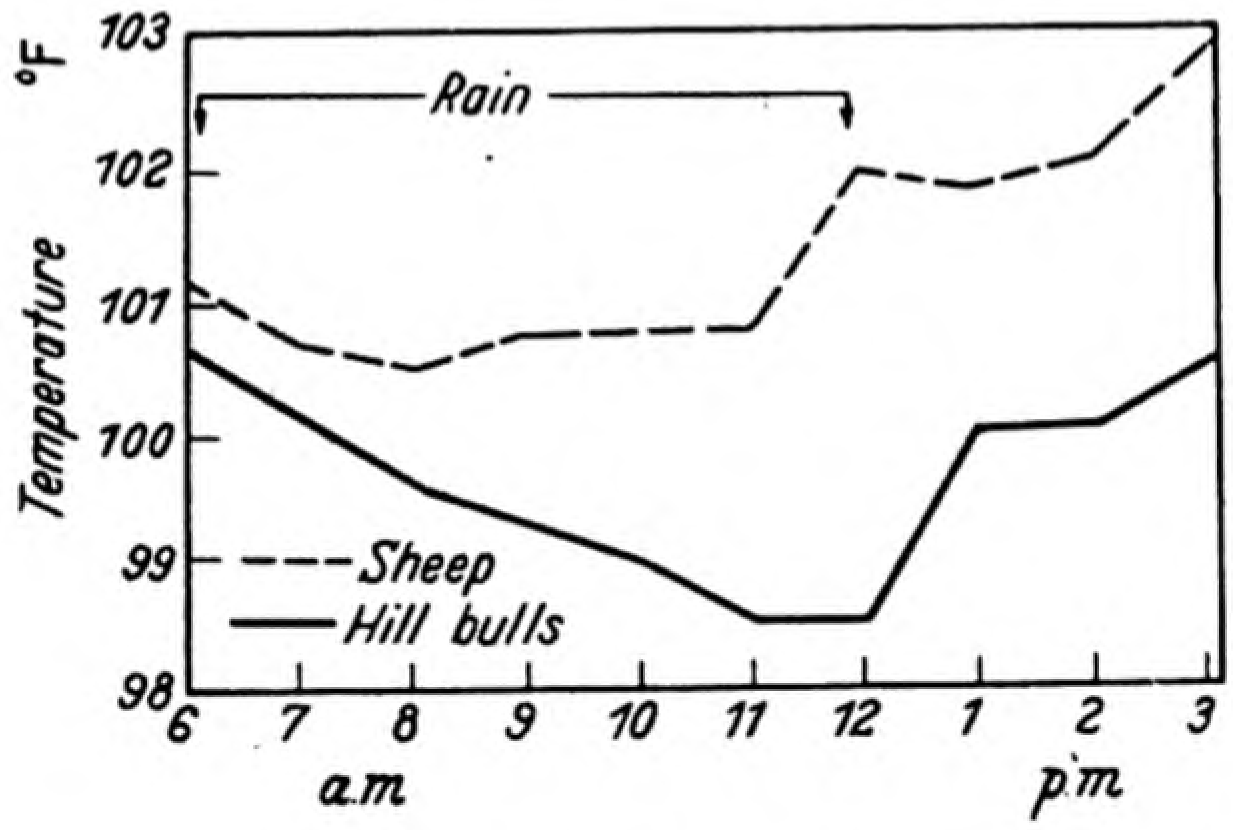


Figure 6.6. The effect of rain on the body temperature of sheep and cattle. The average air temperature was 59°F. and the rainfall 2·9 inches (from Minett, 1947).

Many comparisons have been made between tropical and temperate breeds of cattle both in the field and the laboratory regarding the effect of air temperature on the rectal temperature. *Figure 6.7* strikingly illustrates the influence of tropical blood on the rate of increase of rectal temperature with environmental temperature. The tropically developed Brahman is seen to have maintained its body temperature best, the temperate-bred Aberdeen-Angus least well, while the cross-breeds gave results which lay between those for the other

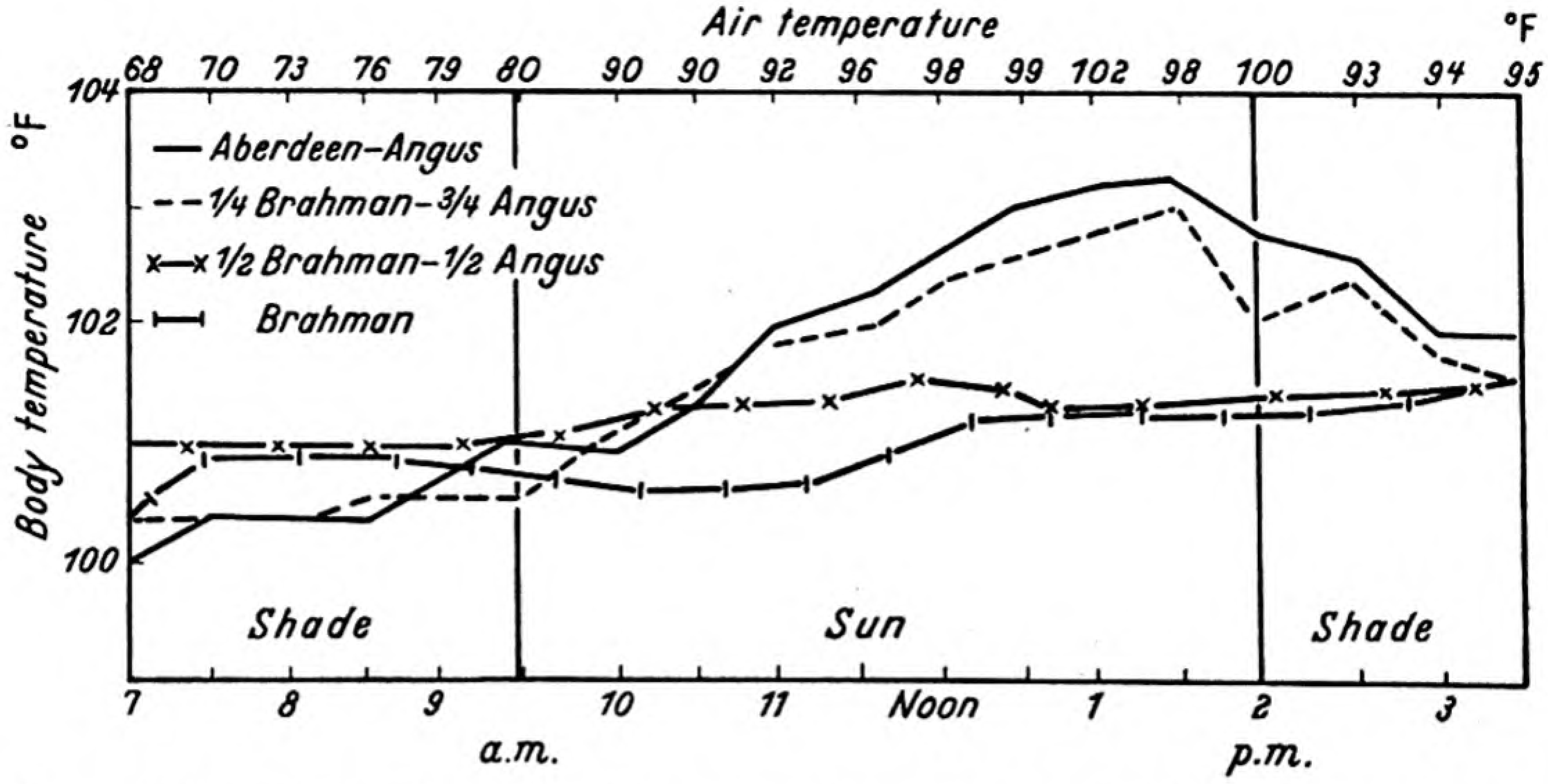


Figure 6.7. The effect of air temperature on the body temperature of temperate, tropical and cross-bred cattle (from Findlay, 1950, by courtesy *Bull. Hannah Dairy Res. Inst.*).

two. On the basis of similar experiments RHOAD (1944) devised the Iberia Heat Tolerance Test by which a heat tolerance coefficient for cattle is calculated from the increase of rectal temperature which occurs during a day in an environment of 90°F. in the sun. Perfect efficiency in maintaining body temperature at 101°F. holds when the adaptability coefficient (A) = 100. On the basis of this test the adaptability of a number of cattle of different breeds has been worked out and is given in Table 6.1. The tolerance of tropical breeds and half-breeds is obviously much higher than any of the pure temperate breeds.

TABLE 6.1

ADAPTABILITY COEFFICIENT OF FEMALE CATTLE AS MEASURED BY THE IBERIA HEAT TOLERANCE TEST—(Data from Rhoad, 1944)

Breeding	*Numbers*		*Adaptability coefficient A**
	Animals	*Tests*	
Brahman	7	18	89
½ Brahman–½ Angus ..	19	67	84
½ Brahman–½ Angus ..	8	21	84
Santa Gertrudis	7	21	82
½ Afrikaner–½ Angus ..	22	64	80
Jersey	34	34	79
¼ Brahman–¾ Angus ..	54	165	77
Hereford	12	12	73
¼ Afrikaner–¾ Angus ..	4	9	72
Angus	31	69	59

* A=100—10 (B.T.—101·0) where B.T. is body temperature of cattle in °F. after a day at 90°F. in the sun.

Other workers have shown that the heat tolerance of an animal as judged by this test increases considerably till after the second year of life. It has also been concluded that the average heat tolerance of a herd of cattle does not change from year to year, and that the adaptability coefficient is unaffected by the stage of lactation or gestation. Laboratory studies by BRODY and his colleagues (KIBLER and BRODY, 1950a, 1951) on Brahman cows and heifers have shown that their rectal temperatures did not begin to rise till an air temperature of 90°F. was exceeded. This result is in accordance with that obtained by field workers.

Very few investigations have been made of the effect of the humidity of the environment on the rectal temperature of cattle. The results which have been obtained are conflicting in their conclusions and further work is required. Of course, in the range of environmental temperature in which evaporation is an important channel of heat loss, *i.e.* in environmental temperatures approaching the skin temperature, raising the humidity of the air markedly affects the rate of rise of rectal temperature with environmental temperature. The effect of increasing the humidity of the air at environmental temperatures from 96 to 104°F. on the rectal temperature of young Ayrshire calves is readily seen from *Figure 6.8*, taken from the present authors' unpublished data. Such high humidities and temperatures are never likely to be encountered in byres in Britain and it would seem likely that even high humidities have little effect on the rectal temperatures of temperate cattle at environmental temperatures of less than about 77°F.

In the present state of knowledge therefore, it would appear that high air temperatures influence the rectal temperature of cattle to a marked degree, the effect being greatest with temperate breeds of cattle and least with tropical breeds and that intermediate breeds fall between the two extremes. Calves are more affected than adult animals and the effect of humidity is only pronounced at temperatures within the zone of evaporative regulation.

The effect of environmental temperature on the rectal temperature of sheep and pigs has not been studied nearly so extensively as in cattle. It appears, however, that sheep are more resistant to the effect of a rise of body temperature than other farm mammals. LEE (1950) has shown that on exposing non-pregnant non-lactating Camden-Park Merino ewes to an air temperature at 104°F. for 7 hours at a time the body temperature increased from 0·5°F. above normal at 15 mm. Hg. vapour pressure to over 2·5°F. above normal at 40 mm. Hg. vapour pressure. Little or no effect of humidity on rectal temperature could be observed at lower air temperatures. Field studies (MILLER and MONGE, 1946) have shown that under the same environmental conditions the highest rectal temperatures were found in Southdown and Hampshire sheep while Merinos exhibited the lowest rectal temperatures with the smallest daily fluctuations. It is clear, therefore, that breed differences to thermal environment exist in sheep as well as in cattle.

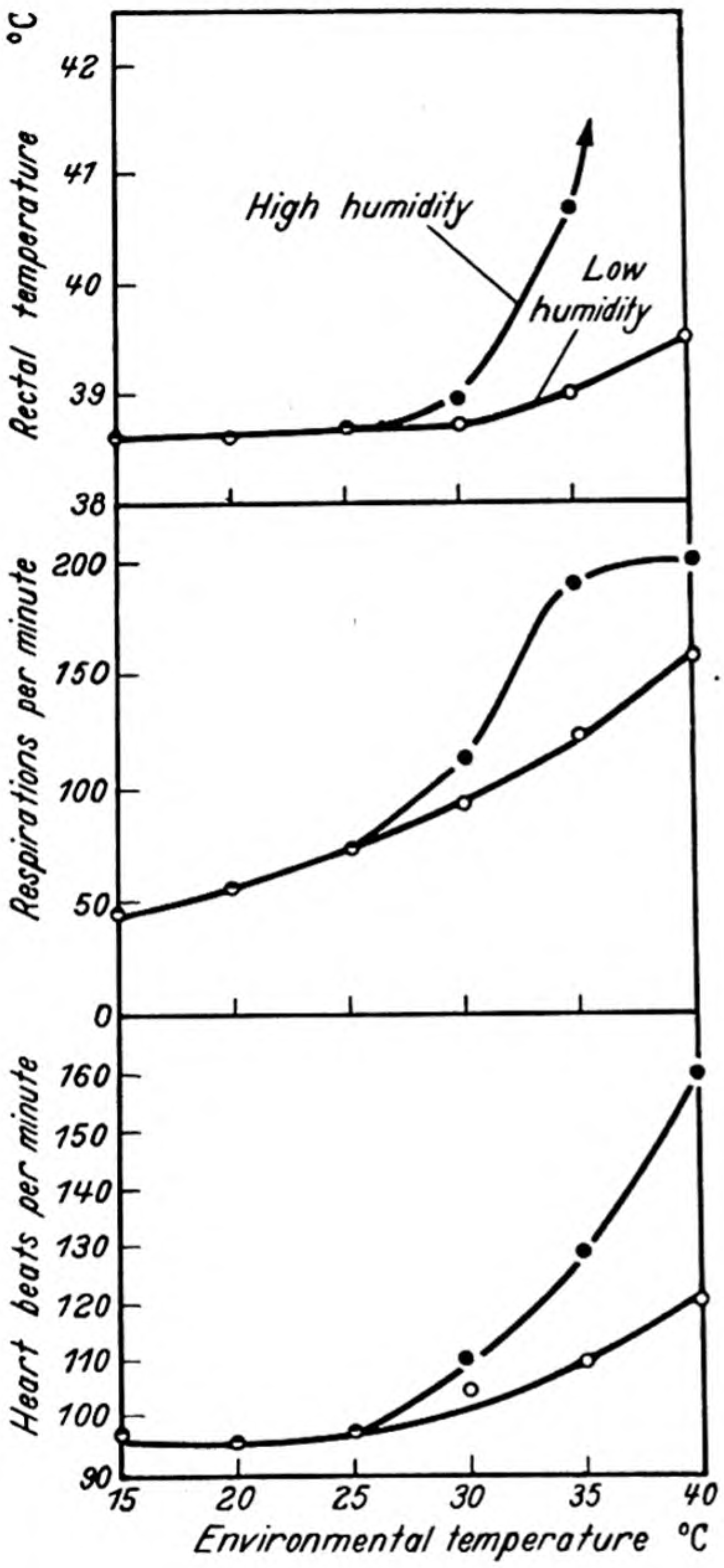


Figure 6.8. The effect of environmental temperature and humidity on the rectal temperature and cardiorespiratory activity of Ayrshire calves. The conditions at low humidity were 17 mg. litre absolute humidity and at high humidity, 6 mg. litre saturation deficit.

The body temperature of the pig is not so stable as that of cattle or sheep. Inadequate thermo-regulation in the pig is well known to good pig breeders who recognize the necessity of providing shade and wallowing water in hot summer weather and artificial warmth in pig rearing houses in cold weather. A range of rectal temperature for the pig from 98·3° to 104°F. has been quoted by Findlay (1950) after examination of the data of numerous workers. Psychrometric room studies on the effects of air temperature and relative humidity on the physiological reactions of swine were made by Heitman and Hughes (1949) who cited most of the relevant literature. They showed that as air temperature increased from 40° to 115°F. the rectal temperature of pigs also increased, the magnitude of the increase being greater the heavier the pig. This effect is shown in *Figure 6.9* taken from data by these workers. Only at temperatures approaching 96°F. could the effect of humidity on rectal temperature be shown. When, at an ambient air temperature of 96°F., the relative humidity was gradually increased during 8 hours' exposure from 30 per cent to 94 per cent the rectal temperature of the pigs increased by 2·5°F. On decreasing the relative humidity to 18 per cent, body temperatures returned to their initial values. These same authors also demonstrated the profound cooling effect of water evaporation. For example, three 240 lb. hogs were kept at a room temperature of 100°F. All were distressed and had an average rectal temperature of 106·8°F. Four litres of water were then poured on

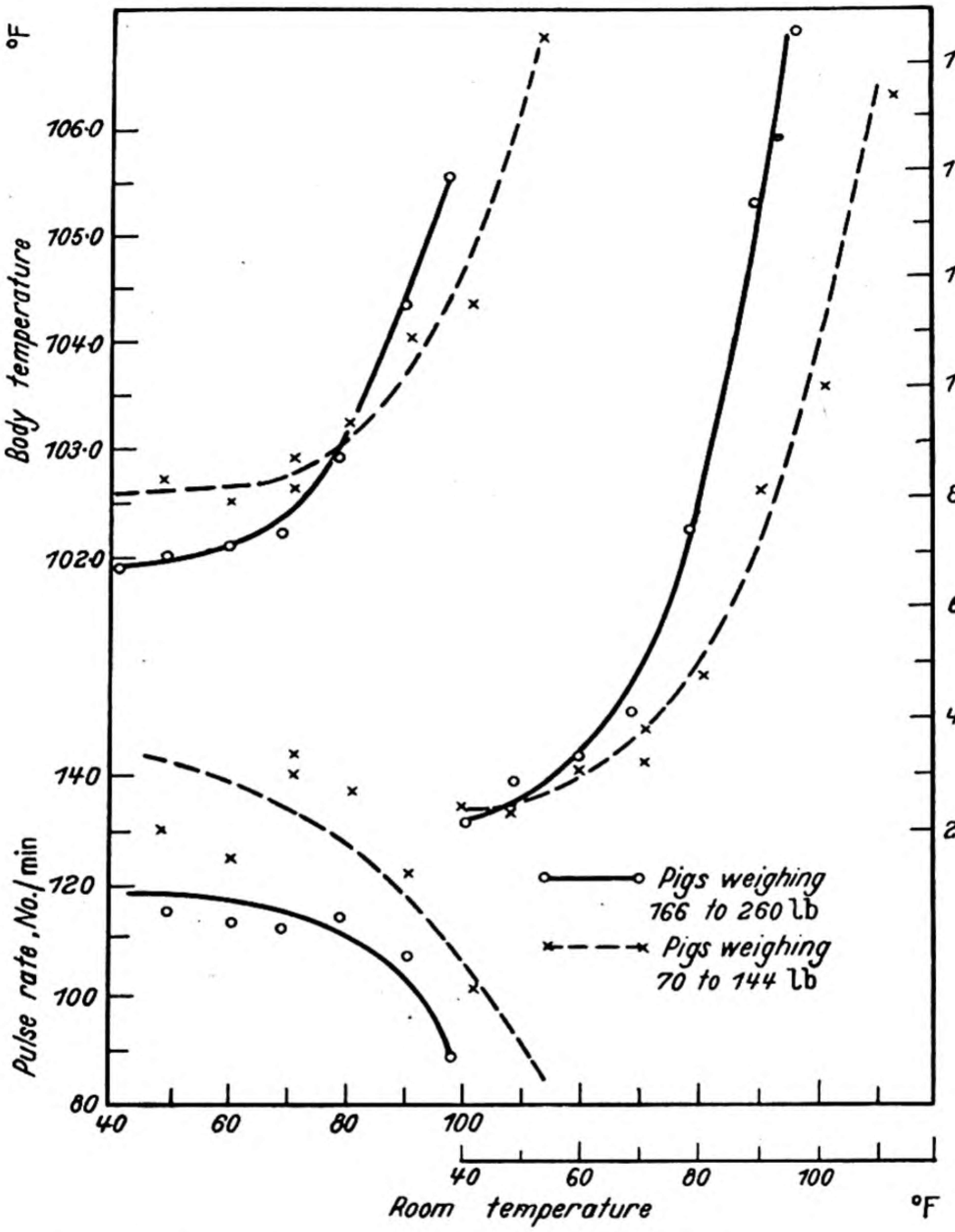


Figure 6.9. The effect of air temperature on the body temperature and cardiorespiratory activities of pigs (from Heitmann and Hughes, 1949, by courtesy *J. Anim. Sci.*).

the dry floor at 100°F. The hogs immediately rolled on the wet floor and within 90 minutes their rectal temperatures were reduced on an average by 2°F. Increasing the air movement in the chamber, still further reduced their rectal temperatures, though increasing air movement on dry pigs did not have this effect. Interesting observations were also made by these authors on the behaviour of pigs at high temperatures. As air temperatures rose about 80°F. the animals became lazy and lay flat on the floor. At high air temperatures, when a pig urinated the others would wallow in the moisture and turn over from time to time to expose their wet side. On wet floors, the hogs tossed from side to side in an effort to keep their wet sides continually exposed. Below 60°F. the swine tended to lie side by side, *i.e.* to huddle or practise ‘ community heating ’.

Other workers (TIDWELL and FLETCHER, 1951) have studied the effect of summer environments on the body temperature of swine. The body temperature of pigs exposed for 15 minutes to sunlight at an air temperature of 88°F. rose 1·2°F. whereas the same pigs at the same temperature not exposed to the sun showed a rise of only 0·9°F. for the same time of exposure.

While heat regulation in the adult pig is poor compared with that of sheep or cattle, heat regulation in the baby pig is much worse and is so poor as to present a serious problem to pig breeders. Excellent work on temperature adaptation in the baby pig has recently been published by NEWLAND, MCMILLEN and REINECKE (1952). They showed that in environmental temperatures ranging from 55° to 75°F. the body temperature of new-born pigs dropped by 3° to 12°F. during the first hour after birth, averaging a drop of about 4°F. as indicated in *Figure 6.10*. The sharpest drop in temperature occurred during the first 20 minutes of life until by the time the pig was an hour old there was a gradual increase to normal. In environments of 60° to 75°F. normality was attained within about 2 days, but in environments of 25° to 35°F. normality was not attained until some 10 days had elapsed. This is illustrated in *Figure 6.11*. When put into an environment having a temperature of 34°F. one-day-old pigs fell into a coma within 2 hours and lay helpless, but they became active and suckled after they had been warmed under a pig brooder for 3 hours. In these experiments it was observed that the heat conservation devices of shivering and pilomotor function were quite well developed in the baby pig when only 1 hour old.

There is a significant correlation between the weight of a pig and its ability to adapt itself to its environment as judged by its ability to maintain a normal body temperature. This is to be expected from the laws stated on page 255 since the lighter pig has proportionately more surface area from which to radiate heat than the larger pig.

These facts indicate that as judged by their ability to maintain a normal body temperature, sheep have the best developed heat regulation system, cattle have one which is not so efficient, whereas pigs have a system which is much inferior to the other two. Recent advances indicate that chilling to 0°F. has little or no effect on body temperature in cattle and this is probably true also of sheep. These animals are well insulated by their hair and wool, unlike the pig, on which chilling has a profound effect, especially in the young. As judged by the ability to maintain a normal body temperature the critical temperatures for adult cattle and for pigs seem to be around 60°F. and 70°F. respectively, though for pigs the range will vary considerably with the weight and physiological state of the animal.

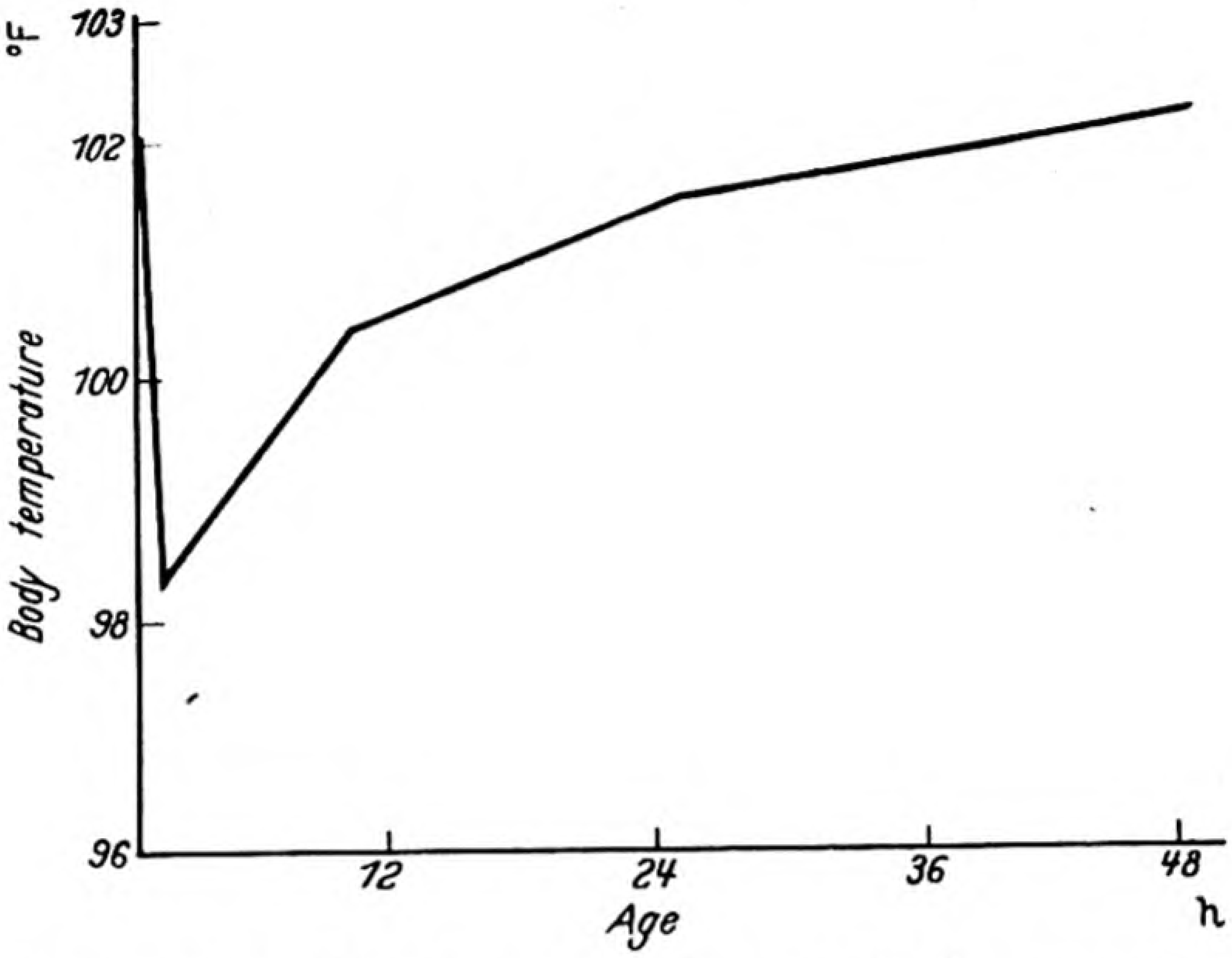


Figure 6.10. Relationship of age to body temperature in 25 pigs up to 48 hours old. Environmental temperature 55° to 75°F. (from Newland, McMillen and Reinecke, 1952, by courtesy *J. Anim. Sci.*).

CARDIORESPIRATORY ACTIVITIES

Respiration Rate

Under the influence of excessive heat burdens, cattle, sheep and pigs exhibit polypnoea to a degree which depends on the magnitude and duration of the heat stress to which they are exposed. Increasing the rate of respiration causes an increased dissipation of heat in two ways ; firstly by warming the inspired air and secondly by increasing evaporation from the respiratory passages and lungs. The heat exchange brought about by warming the inspired air is proportional to the mass of the inspired air, its specific heat and the temperature difference between the inspired and expired air. The heat exchange by evaporation is the product of the mass of water vapour added to the air and the latent heat of evaporation of water.

The effect of thermal environment on the respiration rate has been widely investigated in the field and in the laboratory for cattle, but to a lesser extent for sheep and pigs. This work has been reviewed in detail by **Findlay** (1950, 1953). The main conclusions are presented below.

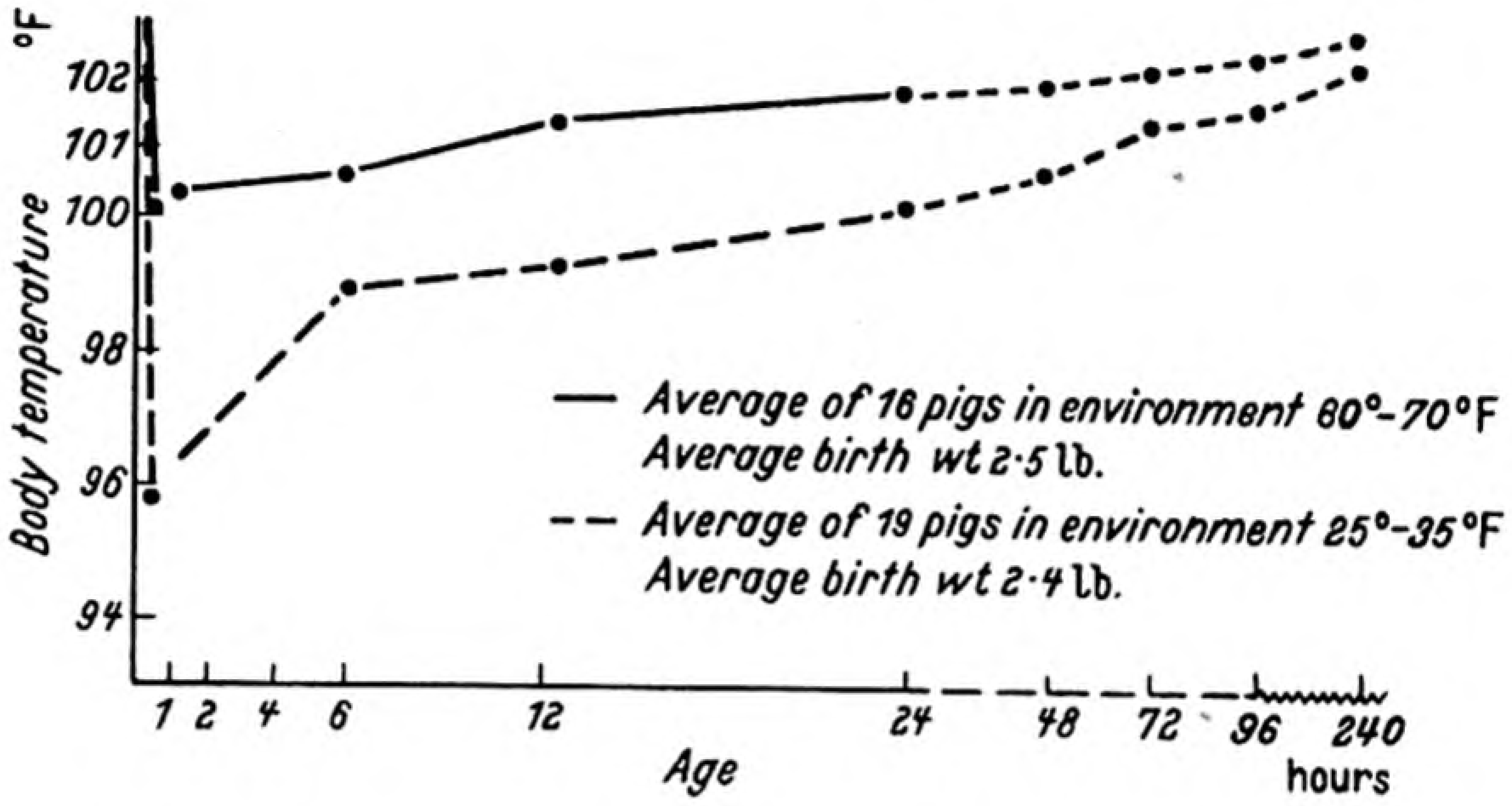


Figure 6.11. A comparison of body temperature drop in pigs raised in warm and cold environments (from Newland, McMillen and Reinecke, 1952, by courtesy, *J. Anim. Sci.*).

Brody and his co-workers (*see* **Findlay**, 1954) have shown that the respiratory rate of cattle rises with increasing air temperature in the range 40° to 105°F., the rise being small at the lower temperature, very great between 80° and 100°F. and tending to reach its maximum value between 100°F. and 105°F. The critical environmental temperatures at which the increase in respiration rate became marked varied with the breed of animal, being 60°F. for Holsteins, 70°F. for Jerseys and 80°F. for Brahmans. Above 80°F. the respiration rates of the Brahmans rose much more rapidly with environmental temperature than did that of the other animals, and at 105°F. exceeded their highest levels. *Figure 6.12* is a composite graph of results obtained in field experiments in the dry tropics. Over the temperature range within which the experiments were performed the results are similar to those obtained by Brody.

As would be expected, the effect of humidity on the respiration rate of cattle is only of importance in the zone of evaporative regulation of body temperature. *Figure 6.8* shows the striking effect of humidity on the respiration rates of Ayrshire calves exposed to environmental temperatures between 96° and 104°F. However, as with rectal temperature, it is unlikely that respiration rate is much affected by humidity at temperatures likely to be encountered in byres in Britain.

Sheep and pigs also exhibit large increases in respiration rate at higher environmental temperatures. The reaction of the pig is illustrated in *Figure 6.9*. It has been shown that there are differences between breeds of pigs exposed to the same conditions in the extent of the increase in their respiration rate with increasing air temperature.

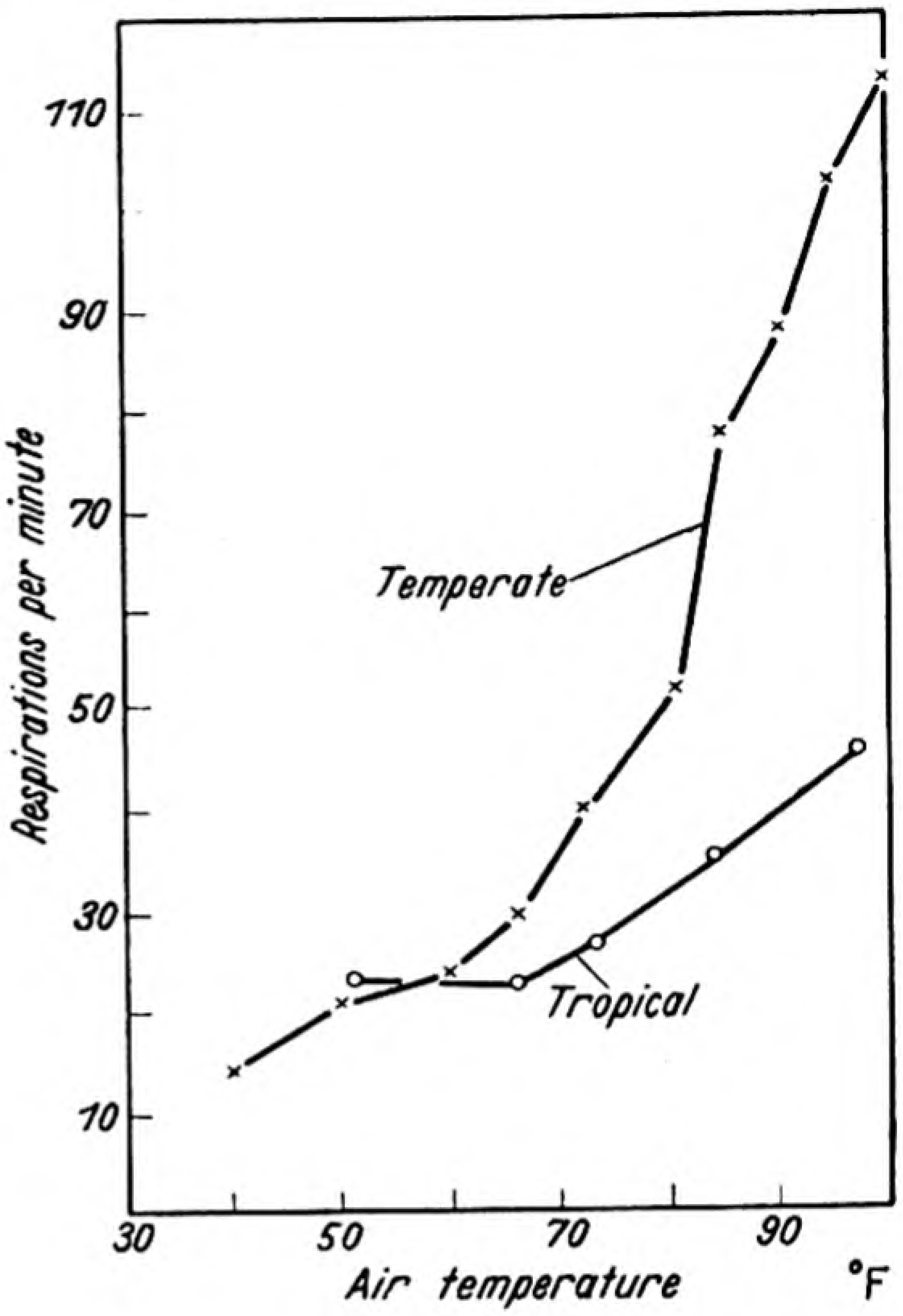


Figure 6.12. A composite graph showing the difference between temperate and tropical cattle in the behaviour of their respiration rates with rising air temperature (from Findlay, 1950, by courtesy *Bull. Hannah Dairy Res. Inst.*).

It may be noted in passing that the increases in respiration rate that occur with increasing air temperature in cattle, sheep and pigs can be very great indeed. Increases for a temperature rise from 60° to 105°F. of up to 200 respirations per minute have been observed by the authors in Ayrshire calves 6 months old.

Temperatures down to 0°F. have little or no effect on the respiration rate of cattle or sheep, though low temperatures, by interfering with the maintenance of normal body temperature in the pig, may affect respiration in pigs to a marked extent.

Heart Rate

Observations made on the heart rate of cattle indicate that it is largely unaffected by temperature, except when the animal is under high thermal stress, *e.g.* at very high ambient temperatures of 100°F. or so. Changes in the pulse rate tend to parallel changes in heat production and food consumption and cannot, from the evidence available, be ascribed to environmental temperature itself. High pulse rates in cattle, are, however, usually associated with abnormally high rectal temperatures of the order of 106°–107°F. Increases in the pulse rate of Ayrshire calves with increasing environmental temperatures are shown in *Figure 6.8*.

The little work which has been done on the pulse rate of sheep in different thermal environments appears to indicate that the heart rate of sheep rises with increasing environmental temperature though the rises noted were very slight (FINDLAY, 1950).

The evidence with regard to the effect of heat on the pulse rate of the pig is conflicting. Some workers have claimed that the heart rate of the pig rises with exposure to increasing environmental temperature, while others, as illustrated in *Figure 6.9* have claimed that the pulse rate of pigs decreases with rises in environmental temperature. However, as with cattle these effects are bound up with changes in heat production and food consumption and cannot be related simply to environmental temperature.

PRODUCTION ACTIVITIES

As already discussed the effect of heat stress on cattle is reflected in the cessation of grazing, *i.e.* in lowered food consumption. With increasing temperatures appetite is depressed, food consumption decreased and heat production consequently reduced. As a result of the decrease in food consumption productivity is affected ; in cows adverse changes occur in the yield and composition of the milk; in pigs growth rate is reduced. Earlier work has been reviewed by FINDLAY (1950). It indicated that at environmental temperatures between 70° and 80°F. milk yield in cattle of temperate breeds was not significantly affected but that the fat percentage of the milk was reduced. Above 80°F. the milk yield declined and as a result of this there was a rise in fat percentage. It was found in this earlier work that at low environmental temperatures with the breeds studied, milk yield was practically unaffected while fat percentage tended to increase.

The most comprehensive work recently carried out on the effect of environmental temperature on productivity is that of BRODY and his collaborators at Missouri: it has been adequately summarized by COBBLE and HERMAN (1951). The effect of temperatures ranging from 5° to 105°F has been studied in a psychrometric laboratory. The principal findings may be summarized as follows:

(1) Milk yields decreased by 50 to 75 per cent at temperatures above 80°F. with Holstein cows and above 85°F. with Jersey cows and with Brown Swiss cows. No effect was noticeable on the milk yield of Brahman cows at these temperatures or at temperatures as high as 90°F. The critical temperature for milk yield decline appeared to be between 70° and 80°F. for Holsteins and Jerseys, and between 85° and 90°F. for Brown Swiss cows.

(2) At 105°F. food consumption virtually ceased in Holsteins and Jerseys, and in Brown Swiss cows amounted to only 1/10th of their

food consumption at 80°F. On lowering the temperature to 50°F. food consumption returned to normal in all animals.

(3) Holstein cows appeared to be unaffected by lowering the temperature to 5°F., though Jerseys showed a slight decrease in milk yield at about 32°F.

These results together with other results previously obtained in field experiments appear to set the optimal temperature for milk yield in cattle of temperate breed at between 50° and 60°F. They certainly indicate that temperatures even as low as 32°F. will have little effect on milk yield whereas temperatures above 60°F. will adversely affect milk yield.

Studies in such detail as those cited, have not been made for either sheep or pigs, though recently HEITMAN and HUGHES (1949) have shown in psychrometric room experiments that swine weighing around 100 lb. utilize food to a greater degree and gain weight more rapidly in the neighbourhood of 75°F. than at other temperatures whereas heavier hogs weighing approximately 200 lb. do better in the region of 60°F. These findings are graphically illustrated in *Figure 6.13.* They agree well with other data in the literature on critical temperatures. Some studies have been made on sheep (MILLER, MONGE and ACCAME, 1944); which suggest that the productivity of sheep as measured in percentage of lambs raised to weaning, average daily gains of lambs to weaning, and fleece weight of ewes, is in the same order as the ability of the ewes to maintain normal body temperature and respiration rate during periods of high atmospheric temperature.

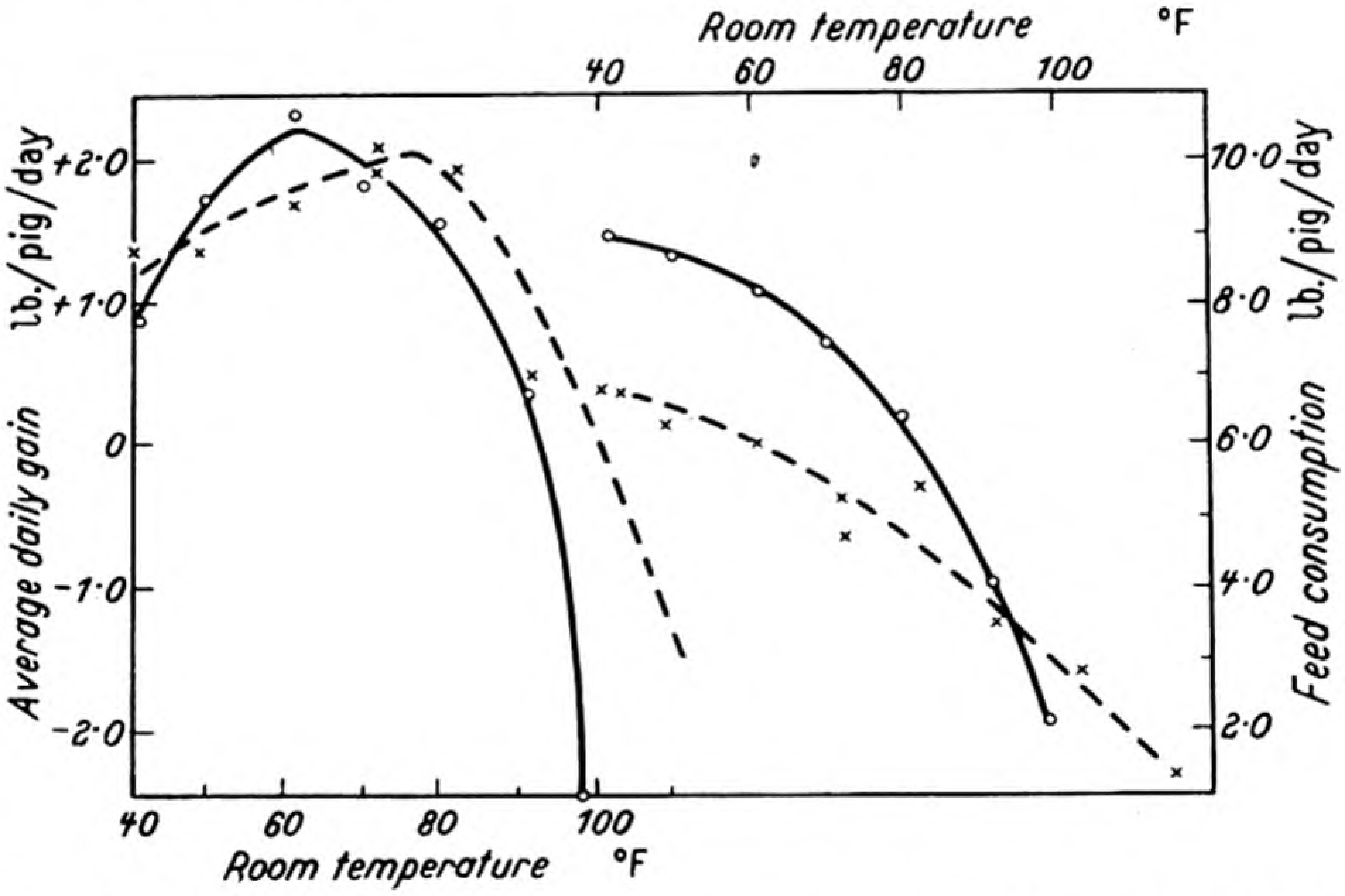


Figure 6.13. The effect of air temperature on the rate of gain and feed consumption of pigs. Broken line = light pigs, other line = heavy pigs (from Heitmann and Hughes, 1949, by courtesy *J. Anim. Sci.*).

Productivity is thus seen to be closely related, in pigs, sheep and cattle, to the efficiency with which a particular animal can maintain its heat regulation.

CHANGES IN THE COMPOSITION OF MILK AND BLOOD INDUCED BY DISTURBANCE OF HEAT REGULATION

With European and Indian-evolved cows subjected to rising temperatures from 80° to 90°F. increases occurred in the total solids and chloride contents of the milk and decreases in the contents of lactose, total nitrogen and total non-fatty solids, the increase in total solids being due almost entirely to the increase in the percentage of fats which accompanied a decrease in yield. High environmental temperatures had no effect on the milk composition of Brahman cows.

In Holstein and Jersey cows decreasing temperatures to 5°F. tended to increase the total solids, solids-not-fat and total nitrogen contents. It may be concluded from this (COBBLE and HERMAN, 1951) and earlier work (*see* FINDLAY, 1950) that environmental temperatures ranging from 30° to 75°F. do not materially affect the milk composition of European breeds, but this is not so for temperatures above and below this range.

Few workers have attempted to assess the effect of environmental temperatures on the blood composition of farm animals. Earlier work (FINDLAY, 1950) indicated that high haemoglobin values are associated with high adaptability to extreme conditions of temperature and this finding for cattle has been confirmed recently (RUSOFF, FRYE and SCOTT, 1951). This is also true of the specific gravity of the blood, the serum Ca: P ratio and the number of erythrocytes. High temperatures appear to cause an increase in the amount of circulating haemoglobin. Sudden falls in temperature have been claimed to cause sharp rises in the leucocyte count of the blood of cattle from temperate regions. The most recent work (BLINCOW and BRODY, 1951) performed in a psychrometric laboratory, under conditions which allowed for acclimatization and which somewhat simulated seasonal temperature change, indicated that for European and Indian evolved cattle no obvious changes in blood composition occur until air temperatures of 65° to 100°F. are reached when there is a large increase in the creatinine content of the blood, amounting to over 100 per cent of the level at 0°F. Between 65° and 100°F. the carbon dioxide combining capacity, ascorbic acid and cholesterol levels in the blood are all reduced to less than half the levels at 50°F. These changes have been interpreted as reflecting refusal or reduction of food with increasing air temperature coupled with the reaction of the pituitary-adrenal system to hunger and heat stress. Contrary to what has been found in man, there were no apparent disturbances in water, electrolyte balance and colloid concentration of the blood on increasing the temperature from 65° to 100°F. The probable reason for this is the fact that very little increase in evaporative loss occurs in cattle above a temperature of 80°F. whereas the evaporative loss in man rises exponentially with increasing environmental temperature above 80°F. (*see* page 289). Haematocrit, erythrocyte and haemoglobin values were found to be higher in the Brahman cows thus substantiating other work.

It has often been asked why the gross hyperpnoea which cows exhibit at high environmental temperatures does not cause alkalosis. As noted in this section the carbon dioxide combining capacity of the blood does in fact fall with increasing environmental temperature and this could be interpreted as a fall in the alkali reserves. However, in the course of experiments in which the CO_2-combining capacity of the blood has been investigated, the feed consumption has also decreased with increasing environmental temperature and it is not therefore possible to say whether hyperventilation *per se* causes an alkalosis in dairy cattle. Had the composition of the blood and urine in terms of their acid-base shifts been studied at the same time the picture would have been clearer, but this has not been done.

Little work in this respect has been done with sheep. ISRAEL (1938) has investigated the effects of environmental temperature, humidity and air movement on the blood morphology and the catalase and lactic acid content of the blood of hybrids of the domesticated fat-rumped sheep and could find no effect in the temperature range 50° to 122°F. High humidity at high temperatures of from 86° to 122°F. did, however, affect the morphology and chemistry of the blood of the sheep.

A similar sparsity of literature exists with regard to pigs. It has been shown in the course of experiments already reviewed on page 268 that in baby pigs chilled to 34°F. there is a significant drop in the blood haematocrit values, though with pigs 10 days old or more chilling causes almost no change in cell concentration. These facts indicate that the young pigs increase the water content of their blood and thereby cause a decrease in their cell concentration. In older pigs there is no shift in water concentration in either direction. The blood dilution shown by the young pigs in these experiments is the reverse of that in animals with a normally functioning temperature regulating mechanism (BARBOUR, 1921; BARBOUR and TOLSTOI, 1923). It has been shown by many workers that dogs, for example, respond to moderately high environmental temperatures by blood dilution and to cold environmental temperatures by blood concentration. Studies in the authors' laboratory on the response of 4-month-old Ayrshire calves to high environmental temperatures have shown that the response of the calf is similar to that of the dog.

Since older pigs show no change in their blood haematocrits it would appear that the development of the temperature regulating mechanism in young pigs is retarded. Judged by changes in blood concentration it appears that temperature regulation in pigs is not fully developed even up to three weeks of age and there are indications that it may not be fully developed even at 8 weeks (Howie *et al*, 1948).

Chilling one-day-old pigs causes an increase to occur in their blood sugar. Pigs fasted 8 hours before chilling show less glucose increase than those fasted 3 and 5 hours before chilling. Increase in blood sugar on exposure to cold is a commonly found phenomenon in warm-blooded animals. The mechanism causing this increase in blood sugar is not known though it probably comes about by stimulation of the adrenal gland as a result of cold exposure. It is almost certainly a defence mechanism against cold.

EFFECT ON HEAT PRODUCTION

Since the heat production of an animal depends on its feed consumption and on its state of productivity, and since both of these are influenced by environmental temperature, it follows that the heat production of farm mammals must be affected by the environmental temperature. Under cold conditions heat production will be increased by the mobilization of body reserves, the eating of more food, the extension of muscular activity, *e.g.* by shivering and by huddling if the animals are in mass. Under warm conditions heat production will be reduced. In the zone of physical regulation of body temperature the animal regulates its temperature without appreciably altering its heat production. The beginning of this zone for steers lies at about 60°F. and for pigs at about 70°F. Most recent work on the effect of environmental temperature on the heat production of cattle comes from the work of Brody and his associates. This work has been reviewed by Findlay (1954). It has been shown that in lactating Jersey and Holstein cows lowering the temperature from 50° to 5°F. caused an increase in heat production associated with some increase in food consumption. The extra heat is probably the result of either increased muscle tone or the specific dynamic action of the food (*see* page 255) or both. The critical temperature for decrease of heat production with rising environmental temperature appeared to be about 80°F. for Jersey and Holstein cows, about 85°F. for Brown Swiss cows and about 95°F. for Brown Swiss heifers. Heat production did not seem to be much affected by environmental temperature in Brahman cows until temperatures of 100°F. were exceeded, though Brahman heifers behaved similarly to Brown Swiss heifers.

In interpreting these results several points must be noted. The observations cited would not be expected on the basis of investigations in human physiology, since, when man's rectal temperature rises as in fever, his heat production increases (Brody, 1945: DuBois, 1948; Robinson, 1949). The decrease in heat production observed with cattle may be explained in terms of decreased food consumption and milk production and perhaps in depressed thyroid activity (Dempsey and Astwood, 1948). Brody *et al* certainly showed that at 50°F. heat production in Brahman cows was about half that in Jersey cows. It also seems probable that the Indian evolved cows have a lower metabolic rate than the European type cows.

The present state of knowledge indicates, therefore, that above the zone of thermoneutrality (40° to 60°F.) European cows tend to decrease their heat production while Brahman cattle appear to be unaffected till about 95°F. is reached.

The literature on this subject for pigs is confusing in its conclusions. Examination of the most recent literature (Heitman and Hughes, 1949; Heitman, Hughes and Kelly, 1951) indicates that heat production in hogs weighing 70–144 lb. probably changes at about 75°F. and for hogs weighing between 166 and 200 lb. at about 60°F. The graphs on which these conclusions are based are shown in *Figure 6.13*.

Much more work will be required, however, before accurate predictions can be made of the effect of environmental temperature on the heat production of pigs. Critical temperatures for increasing heat production ranging from 13°F. to 75°F. depending on the state of feeding of the pig and its weight have been quoted in the literature. The range 60–75°F. may certainly be regarded as a safe and conservative estimate.

So little is known about the effect of environmental temperatures on heat production in sheep that no critical temperature can be stated. It seems probable, however, that as in other respects with regard to heat regulation, the sheep is akin to the cow in that it is well-adapted for cold conditions and ill-adapted for hot conditions.

EFFECT ON WATER CONSUMPTION

Variation in water consumption may be regarded as a method of heat regulation. The rate of moisture vaporization from the body increases with increasing ambient temperature (*see* page 290), and also tends to increase with increasing metabolic rate and therefore with increasing rates of productive processes and consequently with feed consumption. A high producing cow, therefore needs more water than a low producing cow and requires more than the water included in the extra milk. The extra amounts required will be approximately in proportion to the cow's extra feed consumption. Anything which tends to increase body water vaporization will tend to increase water consumption. Indeed, as Barbour (1941) has stated, the homeotherm will tend to sacrifice blood-water homeostasis for temperature homeostasis. The latest summary in regard to the relation of water consumption to milk production in cattle, that of MORRISON (1948), indicates a total water to milk ratio of about 3·4–5·5 to 1 and a free water to milk ratio of 2·3–4·4 to 1. The ratio increases with increasing amounts of protein in the feed. Cows producing over 100 lb. milk a day may consume up to 300 lb. of water per day. Taking the average for a herd, dairy cattle drink 100 to 120 lb. or about 11 gallons of water a day.

The data available for farm animals other than cattle is too scanty for conclusions to be drawn regarding the effect of water consumption on heat regulation.

Very little work on the effect of ambient temperature on the water consumption of cattle has been published until recently. Work by BRODY and his collaborators reviewed by FINDLAY (1954) indicates that for Jersey and Holstein, Brown Swiss and Brahman cows in the temperature range from 0° to 105°F. the water consumption of Jersey and Holstein cows paralleled feed consumption until 80°F. was reached when water consumption tended to increase with increasing temperatures. There were great individual variations in behaviour. The greater the water consumption the less was the rise in rectal temperature and depression in milk production and feed consumption. Unlike the results for man, the urine production, of lowered specific gravity, increased in direct proportion with the increased water consumption on increasing the ambient temperature. This parallelism between urine output and water consumption with increasing ambient temperature suggests that water consumption may be used not simply to avoid dehydration but also to cool the body directly by heating the ingested fluid. THOMPSON, WORSTELL and BRODY (1949) point out that by increasing the water consumption by 24 gallons per day and by changing the temperature of the water from 60°F. to a body temperature of 106°F. about 2,850 kg. cal. per day are removed from the body. Since, in all the animals the frequency of drinking increased with increasing temperature this ‘ condenser-cooling ’ aspect of water in heat regulation would appear to have some substance.

Some of the individual responses brought out in the work of Brody and his collaborators form an interesting basis for speculation. Thus, one Jersey cow behaved in its water drinking pattern very similarly to Brahman cows in that she increased her water consumption with rising temperature above 75°F.—like the Brahman cows—instead of at above 80°F. like her sisters. This consumption rose from 11 gallons a day at 50°F. to 43 gallons a day at 100°F. ambient temperature. Many of the animals in these studies were observed to splash water over themselves suggesting that this may be a behavioural cooling mechanism. This reaction emphasizes the ameliorating effects of wallows and water sprinkling referred to previously on page 267.

A number of experiments have been conducted in the field on the effect of ambient temperature on the drinking habits and water consumption of cattle and of buffaloes (ITTNER, KELLY and BUILBERT, 1951; MULLICK, MURTY and KEHAR, 1952) and the results suggest that the provision of cool drinking water would be of value in mitigating the effects of high environmental temperatures on cattle. In one experiment the provision of refrigerated drinking water was observed to increase considerably the liveweight gains of the cattle to which it was given over that of a similar control group subjected to the same ambient temperatures but not given refrigerated water.

It is seen then, that water consumption may be regarded as a vital heat regulating mechanism in the temperature economy of farm animals and that the provision of adequate supplies of cooled drinking water is essential to maximum productivity in hot climates.

Water vaporization is of major importance in heat regulation and this occurs from the surface of the animal through its skin, and from its respiratory passages. Before assessing the partitioning of moisture vaporization between the respiratory passages and the skin and its function in heat regulation, it is necessary to examine the role of the skin in heat regulation.

THE ROLE OF THE BODY SURFACE OF FARM MAMMALS IN HEAT REGULATION

In cold conditions, in order to preserve homeothermy, farm animals must conserve heat, and in hot conditions dissipate it. Heat is generated in the deep core of the animal and transferred to its surface through its tissues by conduction and through its blood stream by convection. The transport of heat from the core of the animal will depend on the temperature difference between the animal's surface and its deep core and, where peripheral blood flow is minimal, to some extent on the thermal conductivity of its tissues. The animal modifies this loss of heat or its conservation by alterations in its peripheral blood supply.

Little is known of the transfer of heat from the deep core to the periphery in farm mammals though there is a considerable volume of work in this respect in human physiology. For information on the physical factors governing such transfers in man the reader is referred to HARDY (1949) and BAZETT (1949).

The vascular supply to the skin of cattle has recently been very fully investigated by GOODALL and YANG (1954). These authors showed that there are three vascular plexuses in cattle skin comparable to those in human skin. There is, however, one essential difference. Whereas the arteries of the cutaneous arteriolar plexuses and the veins of the venous plexuses run independently of each other in human skin, in cattle skin the arteries and veins of the corresponding plexuses always run together. Many of the larger arteries, in fact, in bovine skin are accompanied by two veins. This is a most significant finding whose importance in heat regulation in cattle cannot be overestimated.

As recognized as early as 1876 by CLAUDE BERNARD and commented on recently by BAZETT (1949) the interchange of heat between an artery and its accompanying vein or veins, *i.e. venae comites*, plays an important part in the conservation of heat in the body. The warm blood in the artery going towards the periphery is cooled by the venous blood returning from the skin and so the temperature gradient at the skin surface is reduced and less heat is lost to the environment. Whereas in the human these *venae comites* seem to be present only in conjunction with the large arteries of the limbs, *e.g.* the femoral, radial, *etc.*, yet in cattle they appear to be almost universally distributed throughout the skin. It thus appears that on an anatomical basis temperate cattle—for the cattle used in these studies were Ayrshires—are extremely well-adapted to a cold environment. Thus, although the rich capillary blood supply to the skin of cattle, especially in the sub-epidermal region, would lead one to suppose that the skin was a highly effective organ for dissipating heat, yet the widespread distribution of *venae comites* casts doubt on this supposition.

A further important point emerges from the work of GOODALL and YANG (1954). They found that on perfusion of the intercostal arteries with Indian ink a large area of skin on the back and flanks was widely perfused. This means that certainly most of the blood reaching those areas of skin must first have passed through the intercostal muscles, and the venous return to the heart and hence to the lungs must have been by a similar path. BAZETT (1927), considering the dissipation of heat during heavy exercise, points out that the skin over active muscles shows an increase in temperature long before there is an increase in rectal temperature. The interchange of heat between the intercostal muscles and the blood in both arteries and veins must therefore play an important part in the heat regulation of cattle. When it is considered further that the most active muscles in cattle when they are under heat stress are the intercostals (since as shown on page 270 polypnoea is a first line defence mechanism against heat stress in the bovine), the importance of this finding needs no emphasis.

In cold, man, in order to conserve heat reduces peripheral blood flow through vaso-constriction and in hot conditions increases heat loss by peripheral vaso-dilatation. In parts poorly insulated with hair, *e.g.* the ears, some physiological device is necessary to prevent frostbite in extreme cold. A rapid flow of blood is often used to combat extreme cold, for example in birds' legs (GRANT and BLAND, 1931). The body, however, may risk peripheral frostbite in order to conserve the heat of vital central organs. When arterioles are dilated, especially in the extremities and in parts not well insulated, the anatomical peculiarity of arterio-venous anastomoses, which are small short-circuits between arterioles and venules, serve to increase the flow of blood whenever there is dilation of vessels whether from heat or from the hyperaemia of cold. These arterio-venous anastomoses are known to occur in the ear of the rabbit and have been described by GRANT (1930). Very recently GOODALL (1954) has conclusively demonstrated that the ear of the Ayrshire calf contains many such anastomoses and it is probable that in this thinly insulated tissue their function is the same as that described for arterio-venous anastomoses by Grant. It has been noted that peripheral blood flow is varied according to the needs of heat loss or conservation and this vascular control is a paramount heat regulation mechanism.

There are no studies known to the writers on peripheral blood flow in farm animals, but certain deductions may be made from surface temperature studies in highly vascular tissues. One such study has been made by BEAKLEY (1953). An Ayrshire calf was exposed to an environmental temperature of 12°C. and the environmental temperature was then allowed to rise slowly under controlled conditions. Thermocouples were attached to the ears of the calf to measure their surface temperature. The rectal temperature and environmental temperature were simultaneously measured. *Figure 6.14* illustrates the result obtained. It will be seen that the animal's ear temperature varied to begin with, but at an environmental temperature of 18°C. it suddenly rose to a value of 35°C. Table 6.2 shows the conditions before and after the change:

TABLE 6·2

TEMPERATURES (°C.) IN AN AYRSHIRE CALF BEFORE AND AFTER AN ENVIRONMENTAL TEMPERATURE OF 18°C.

	Before	*After*
Environmental temperature	18	20
Right ear temperature	22	35
Rectal temperature	38	38
Ear temperature—environmental temperature (a)	4	15
Rectal temperature—ear temperature (b)	16	3
Ratio b/a	4	1/5

The ratios b/a are the ratios of the thermal conductances from ear to environment and from body to ear. Since the former conductance must remain constant, the latter changed by a factor of 20. Such a change is equivalent to a 20-fold increase in blood flow to the ear and indicates that the ear may perform the same thermoregulatory function in the calf as the extremities do in man.

It is seen then, that heat is transferred from the centres of heat production in the core of the animal to its periphery by the blood and that this transference is modified by various anatomical arrangements.

The exchange of heat at the surface of the skin may now be considered in the light of recent knowledge.

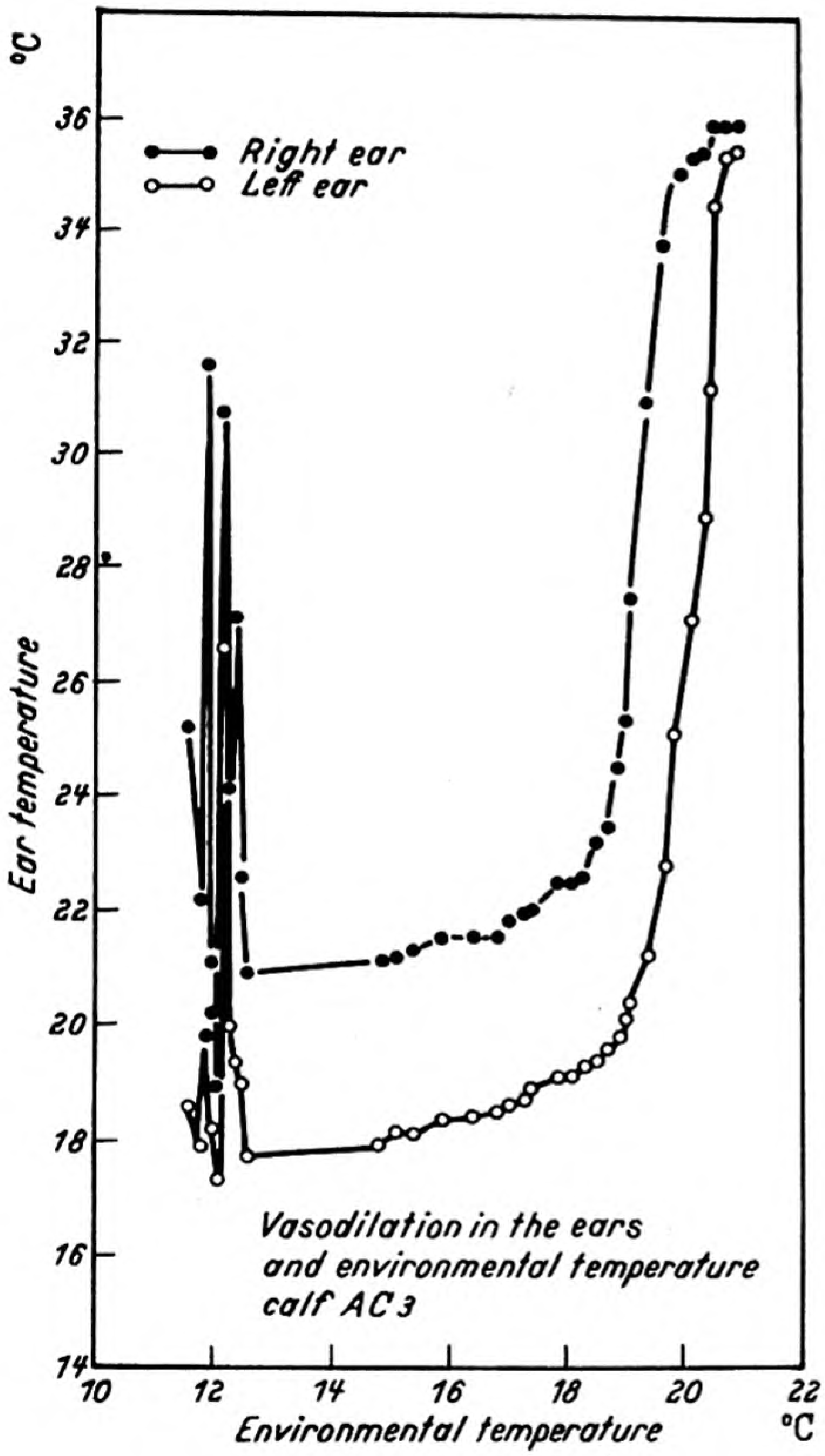


Figure 6.14. The effect of environmental temperature on the surface temperature of the pinnae of the right and left ears of an Ayrshire calf, showing the onset of vasodilation in the ear (from Beakley, 1953).

EXCHANGE OF HEAT AT THE BODY SURFACE

It has been shown that heat arrives at the body surface by vascular routes and it is there conveyed away by convection, radiation, conduction and evaporation. Before considering the various qualities of an animal's surface which affect this heat exchange it will be well to consider present knowledge regarding evaporative loss from the skin of farm animals. Much has been published on the mechanism of sweating and its anatomy in man, but until recently little attention has been paid to the anatomy of sweat glands in farm animals. The physiological evidence for the existence of sweating will be discussed in the next section: only the histological position will be examined here. Findlay reviewed the literature on this subject up to 1950, and a recent series of paper has added considerably to the knowledge (FINDLAY and YANG, 1948, 1951; FINDLAY, GOODALL and YANG, 1950; GOODALL and YANG, 1952; YANG, 1952; VILLARES and BERTHET, 1951a, b). This work has shown that cattle of both temperate and tropical breeds possess so-called sweat glands distributed in much the same way over the entire body surface. One sweat gland is associated with every hair follicle. These glands have a poor blood supply and are apocrine in nature. The histological evidence of their structure, their mode of secretion and the contents of their lumens is such as to make it appear that they are poorly functioning glands from an evaporative point of view, though they are not vestigial structures. Glands very similar to those described by the authors cited for cattle have been described by others in sheep and in swine (ELLENBERGER, 1906; TRAUTMANN and FIEBIGER, 1949). It is important to observe, however, that anatomically the sweat glands of cattle are akin to those of cats, dogs, sheep and swine and not to those of man who possesses highly active eccrine-type glands, whose principle function is in heat dissipation. Water may, nevertheless, be transpired through the skin by simple osmosis, *i.e.* insensible perspiration, in which process sweat glands play no part.

Several characteristics of the body surface of farm animals influence the exchange of heat between the surface and the environment. These factors are the colour of the skin and of its covering, the physical nature of the covering and its state and the orientation of the covering to its surroundings.

THE COLOUR AND NATURE OF THE COVERING

The amount of solar radiation that is absorbed by the coat of an animal is determined to some extent by the colour of the coat. About half the energy in the solar spectrum is in the visible portion. The proportion of this which is absorbed on to the coat of the animal can be gauged roughly by the colour of the coat. A white surface may absorb only 20 per cent of the visible radiation falling on it while a black surface may absorb up to 100 per cent. The other half of the energy contained in the solar spectrum is in the invisible infra-red and is completely absorbed by the coat. Colour thus only affects the total absorption of solar radiation to about half the extent as judged visually. The colour of the skin as distinct from the colour of the coat is also of importance in terms of susceptibility to sunburn and photosensitization, and in lightly haired farm mammals such as the pig, the argument applying to the coat will, of course, apply to the skin. It must not be supposed that all the radiation falling on the coat of an animal is necessarily absorbed by the animal since it may be absorbed in the tips of the hairs and then be dissipated by convection before reaching the animal's skin. The length of the hairs, therefore, will also influence the absorption of radiant heat by the animal.

The effect of the colour of the coat on the absorption of radiation has been reviewed by Findlay (1950, 1954). The results of work on the colour of the coat of cattle indicates that a white, yellow or red coat with a smooth and glossy texture is best for minimizing the adverse effects of solar radiation. The influence of colour of coat on the reflectivity of sunlight from cattle is well illustrated in *Figure 6.15* which shows that more sunlight is reflected from light than from dark coloured coats. It will be seen also that a higher proportion of incident sunlight was reflected by both Afrikaner and Jersey cattle in summer than in winter, regardless of the colour of coat. In winter Jersey cattle reflected slightly more sunlight than Afrikaner cattle. These differences are probably due to differences in the sheen and gloss of the coats since in summer both breeds of cattle had glossy coats with short hair while in winter the Jerseys were groomed but

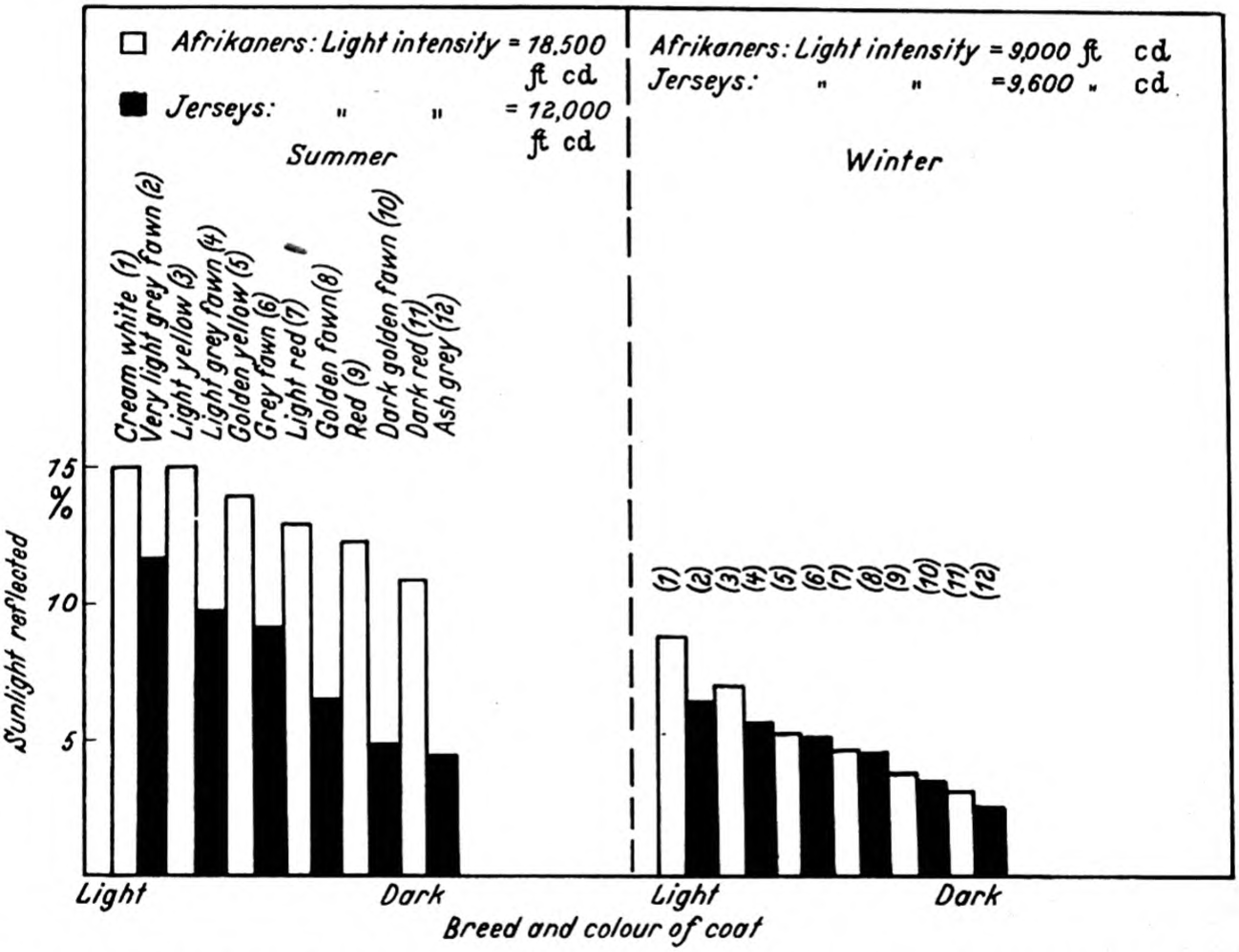


Figure 6.15. The reflection of sunlight from differently coloured coats in Afrikaner and Jersey cattle in winter and summer (from Findlay, 1950, by courtesy *Bull. Hannah Dairy Res. Inst.*).

not the Afrikaners. That these differences in the sheen and texture of the coat affect heat regulation may be clearly seen from *Figure 6.16*. The woolly coated cattle under the same conditions of temperature had a higher respiration rate than the glossy-coated cattle, indicating that they were having greater difficulty in preserving a heat balance. BONSMA (1949) has commented at length on the effect of coat-cover on heat tolerance.

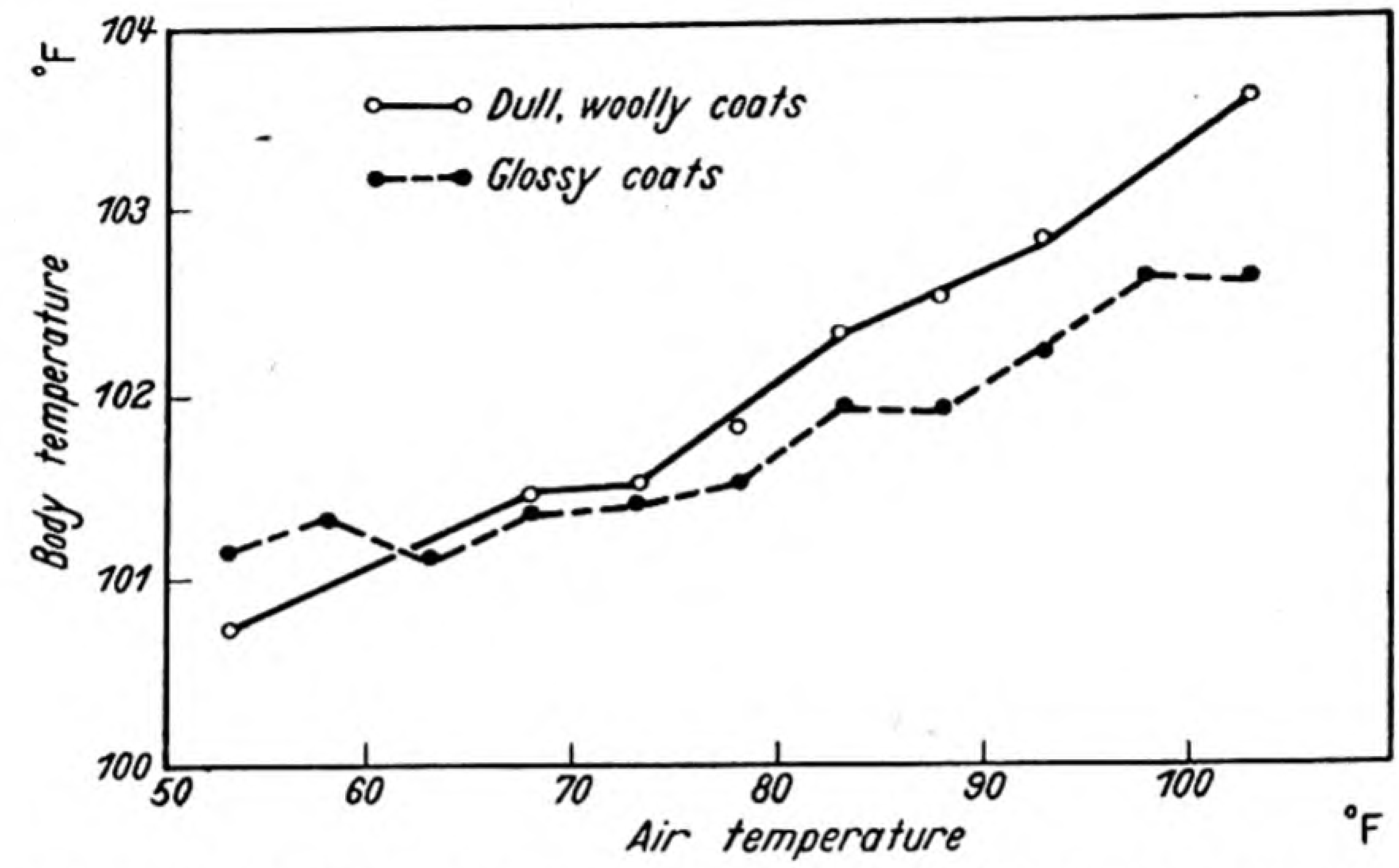


Figure 6.16. The effect of environmental temperature on the body temperature of woolly and glossy-coated cattle (from Bonsma and Pretorius, 1943, by courtesy *Fmg. in S. Africa*).

Table 6·3 illustrates the order of absorptivity that may be expected from differently coloured coats.

TABLE 6·3

THE MEAN ABSORPTIVITY TO SOLAR RADIATION OF HIDES OF DIFFERENT COLOURS (From Riemerschmid and Elder, 1945)

	White Zulu	*Cream Simmenthaler*	*Red Afrikaner*	*Dark Red Sussex*	*Black Aberdeen Angus*
Mean Absorptivity (%)	49	50	78	83	89

It has been shown that the absorptivity of a coat is unaffected by smoothing down or ruffling up and is the same whether the hide is living or dead.

The importance of shade for cattle in the tropics is emphasized by these studies. RIEMERSCHMID (1943) has stated that in direct sunlight the solar radiation absorbed on the coat of a brown coloured cow was approximately three times its own heat production. Shade reduced this radiation load by over 70 per cent.

No work comparable to that outlined for cattle has been reported for other farm animals, though much the same considerations will apply to the sheep. The pig will be in a considerably worse position since it has little protective coat and most of the radiation will be directly absorbed.

The measurement of actual radiation exchange between a farm animal and its surroundings is exceedingly complex and cannot be dealt with here. The magnitude of the problem may be gauged from *Figure 6.17*, showing the radiation exchange patterns that must be considered in open terrain for a sheep. HARDY (1949) and LEE (1954) should be consulted for methods of studying this problem.

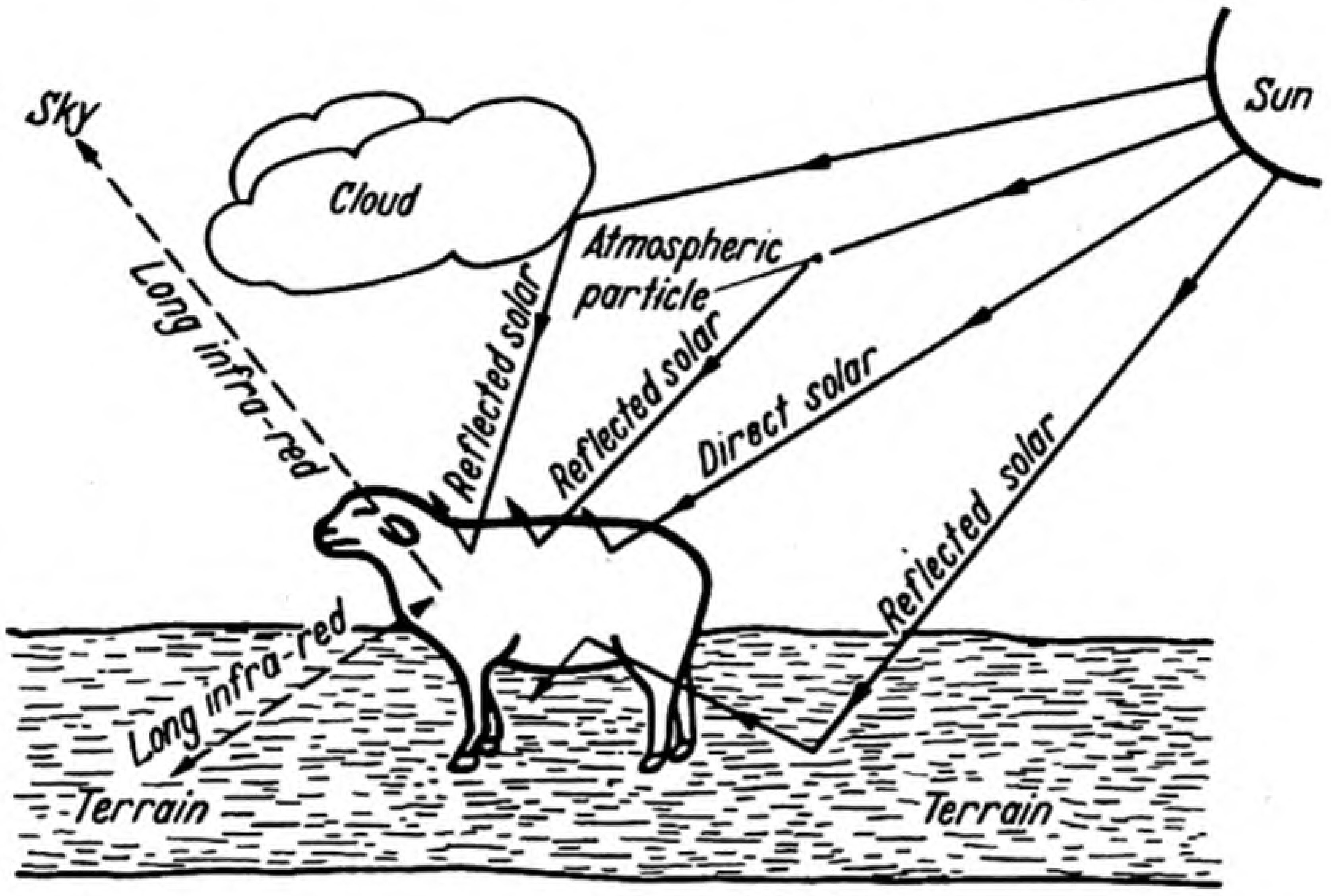


Figure 6.17. The radiation exchange pattern of a sheep in open terrain (from Lee, 1954, by courtesy F.A.O.).

Quite apart from radiation exchange, the nature of the coat will influence considerably convective and evaporative loss from the skin by entrapping air and moisture in the hair mesh. This will slow down convection exchange and provide a local climate of high humidity and so render the exchange of heat by vaporization of water from the skin surface more difficult. Such high humidity gradients have been demonstrated in the sheep by CRAGG and DAVIES (1947).

HEAT REGULATION AND THE SCROTUM

The temperature regulation of the scrotum is unique and is of practical importance since it is known that spermatogenesis is adversely affected by high testicular temperatures.

Under normal environmental conditions the scrotum acts as a thermostat which attempts to maintain a fairly constant thermal environment for the testicles. The scrotal skin temperatures and intra-testicular temperature of the bull exposed to various environmental conditions and the relation between these temperatures and the temperature of the skin and the rectum have been investigated by RIEMERSCHMID and QUINLAN (1941) and by QUINLAN and RIEMERSCHMID (1941). These authors concluded that the heat regulating mechanism of the scrotum was extraordinarily efficient in maintaining the testicular and scrotal-surface temperatures within a very narrow range at air temperatures from 50° to 104°F. They showed, for example, that for a range of air temperature from 59° to 100°F. the intra-testicular temperature varied only from about 95° to 98·5°F. It would appear that this efficiency is not purely physical, *i.e.* due to the action of air temperature on the contracted or relaxed scrotum, but that vascular reaction probably also accompanies scrotal contraction and relaxation. When bulls with pendulous scrotums lie in the sun the temperature of the scrotum may rise by coming in contact with hot ground. Beakley (1953) has shown that scrotal surface temperatures for young Ayrshire calves exposed to temperatures from 68° to 104°F. consistently remain below the air temperature, and also below the general surface temperature of the body and the rectal temperature.

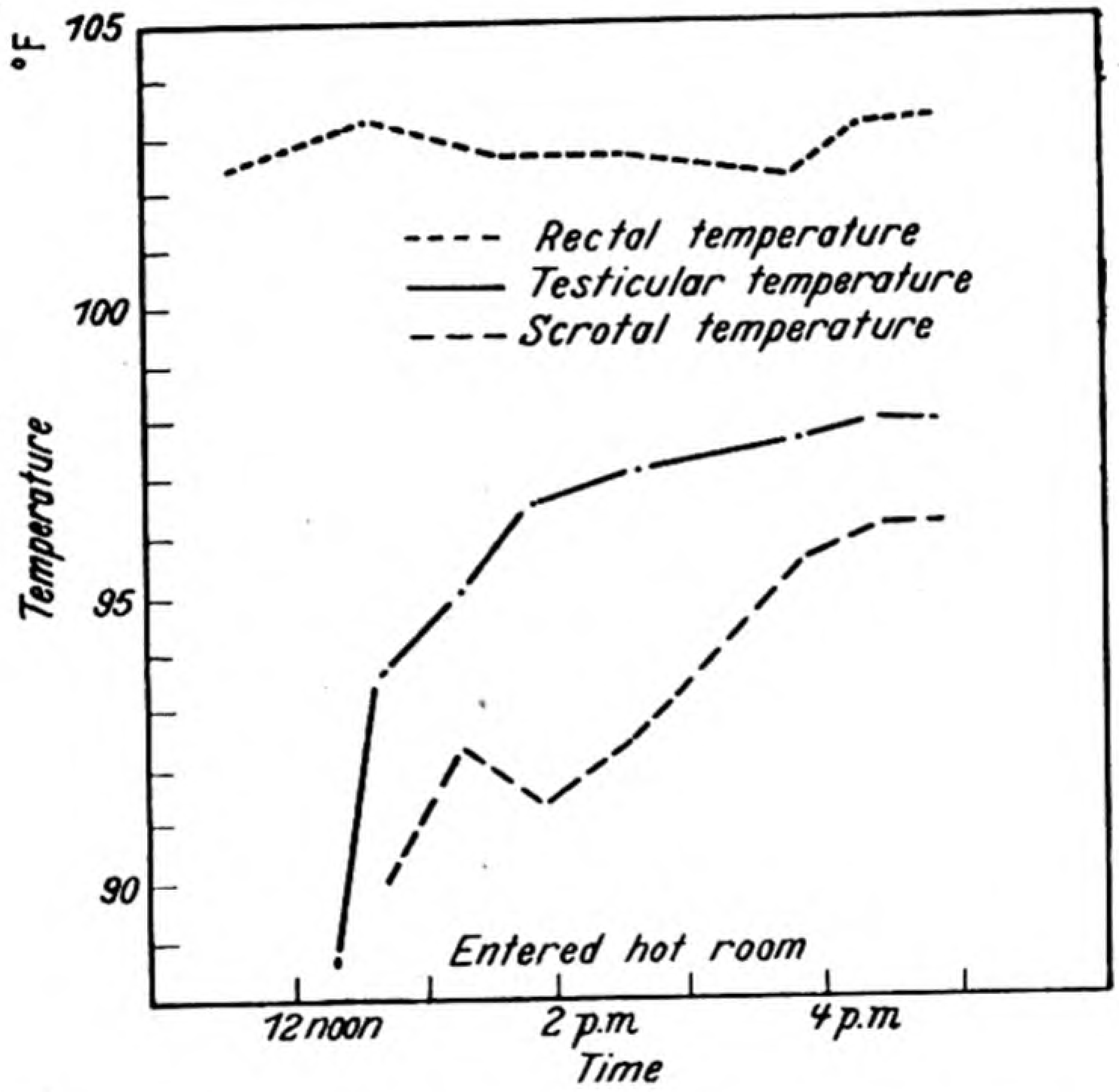


Figure 6.18. The rectal, testicular and scrotal temperatures of a ram exposed to environmental conditions of 102°F. dry bulb and 82°F. wet bulb temperature (from Moule and Knapp, 1950, by courtesy *Aust. J. Agric. Res.*).

There are a number of authoritative papers which give extensive bibliographies on the subject of temperature regulation in relation to the scrotum of rams (Phillips and McKenzie, 1934 ; Harrison and Weiner, 1949; Moule and Knapp, 1950). These papers indicate that a most important role is played by the tunica dartos muscle in maintaining heat regulation in the scrotum by its action in altering the effective area of the scrotum. Some unique features of the vascular architecture of the scrotum also play their part in its efficient heat regulation. The testicular artery takes a long intra-abdominal course, is highly convoluted and is of small calibre. These features would tend to slow down blood flow and be advantageous for the cooling of arterial blood. The arterio-venous relationships in the cord also help. The venous plexus is closely in contact with the artery thus making an efficient heat exchanger. The close proximity of the arterial and venous blood streams in the cord is akin to the function of *venae comites* already dealt with on page 280 and serves to bring the whole testis to a temperature intermediate between that of the abdomen and the surface of the testis and cord. These various anatomical structures have been conclusively shown to perform the functions attributed to them by HARRISON and WEINER (1949). They also probably protect the testis from general increases in body temperature, *e.g.* in hyperpyrexia of fever.

The most recent observations indicate that sweating may play an important part in regulating the temperature of the scrotum. *Figure 6.18* from the data of MOULE and KNAPP (1950) for Merino rams indicates the effectiveness of heat regulation in the scrotum on exposure to a hot climate. It will be seen that both scrotal and testicular temperature remain throughout the experiment much below rectal temperature.

QUANTITATIVE ASPECTS OF HEAT LOSS FROM THE BODY SURFACE AND RESPIRATORY TRACT

Only the general qualitative relations of the respiratory tract and body surface to heat loss have thus far been considered. Very little of a quantitative nature is known of the heat exchange effected by radiation, convection, and evaporation from the skin and respiratory passages of farm animals, *e.g.* the partitioning of heat loss between the skin and respiratory tract or the quantitative effects of humidity on such losses. Most of the work of value has been done very recently with cattle; little is known with regard to other farm animals. This quantitative aspect is of great importance since it bears directly on ventilation standards for byres in temperate countries and on ameliorative measures against heat stress for farm animals in tropical areas of the world.

There are two fundamental ways in which cattle and other farm animals differ from man in their heat loss mechanisms. Firstly, as already noted, they do not appear to possess such a highly developed sweating mechanism as man. Secondly, cattle have a pulmonary ventilation rate about twice as great as man below a temperature of 80°F. (BRODY, 1945). This latter fact naturally gives to cattle a greater respiratory advantage than to man at temperatures below 80°F.

Recent work (**Kibler** and **Brody**, 1950b; **Thompson, McCroskey** and **Brody**, 1949, 1951) has shown that for European evolved cattle, insensible losses vary with surface area rather than with body weight. For both European and Indian evolved cattle the ratio of evaporative loss to total heat production is the same for all animals and increases exponentially with environmental temperature up to 85°F. regardless of breed, weight and productive level. This ratio is higher for cattle than for man at temperatures below 80°F. at which temperature the ratio for man greatly increases. It becomes greater than that for cattle at about 90°F. and far exceeds the ratio for cattle at 100–105°F. environmental temperature.

The vaporized moisture on the basis of moisture loss per animal, whether calculated in grammes per unit surface area or per unit weight of animal is lower for European than for Indian evolved cattle. This is probably due to the lower total heat production of the Indian cattle and possibly to the latter's relatively greater surface area.

The variation in total moisture loss with varying environmental temperature for different weights of Holstein and Jersey cows has been worked out by Brody and his colleagues. Table 6.4 gives an example from their results.

Table 6.4

VARIATION IN TOTAL MOISTURE LOSS FOR DIFFERENT ENVIRONMENTAL TEMPERATURES (From prediction curves given by Thompson, McCroskey and Brody (1951) for lactating Jersey and Holstein cows of 1,000 lb. weight)

Temperature °F.	*Moisture evaporated in lb./cow/hr.*	*Temperature °F.*	*Moisture evaporated in lb./cow/hr.*
0	0·30	60	0·80
10	0·35	70	1·40
20	0·40	80	1·73
30	0·45	90	1·73
40	0·53	100	1·60
50	0·61	105	1·92

From these figures it will be seen that in a byre holding, say 30 cows, and kept at the optimal temperature of 60°F., the ventilating system of the byre will have to be capable of getting rid of 24 lb. moisture per hour exclusive of that contained in the faeces and urine. It may be noted that between 60° and 70°F. the moisture production almost doubles. This stresses the importance of not exceeding the optimal temperature of 60°F. ' A is apparent from all the work on cattle reviewed in this chapter heat, not cold, is the danger in cattle shelters.

Brody *et al* showed that for European cattle as the air temperature rises from 5° to 95°F. the heat lost by respiratory vaporization rises from 4 per cent to 30 per cent of the total heat dissipated. There were no breed differences in the specific humidity of the expired air so that for all breeds respiratory vaporization rate at a given temperature tended to be proportional to the pulmonary ventilation rate of the animal.

Between 5° and 60°F. the vaporization rate from the skin surface of European type cattle was found to be about the same order as the respiratory vaporization rate, but between 60° and 80°F. the body surface vaporization rate increased fourfold. At 95°F. in lactating dairy cows of European type—Jerseys and Holsteins—approximately 26 per cent of the heat was dissipated by vaporization from the respiratory tract, about 59 per cent by vaporization from the outer body surface and about 15 per cent by non-evaporative cooling. These relationships are illustrated in *Figure 6.19*.

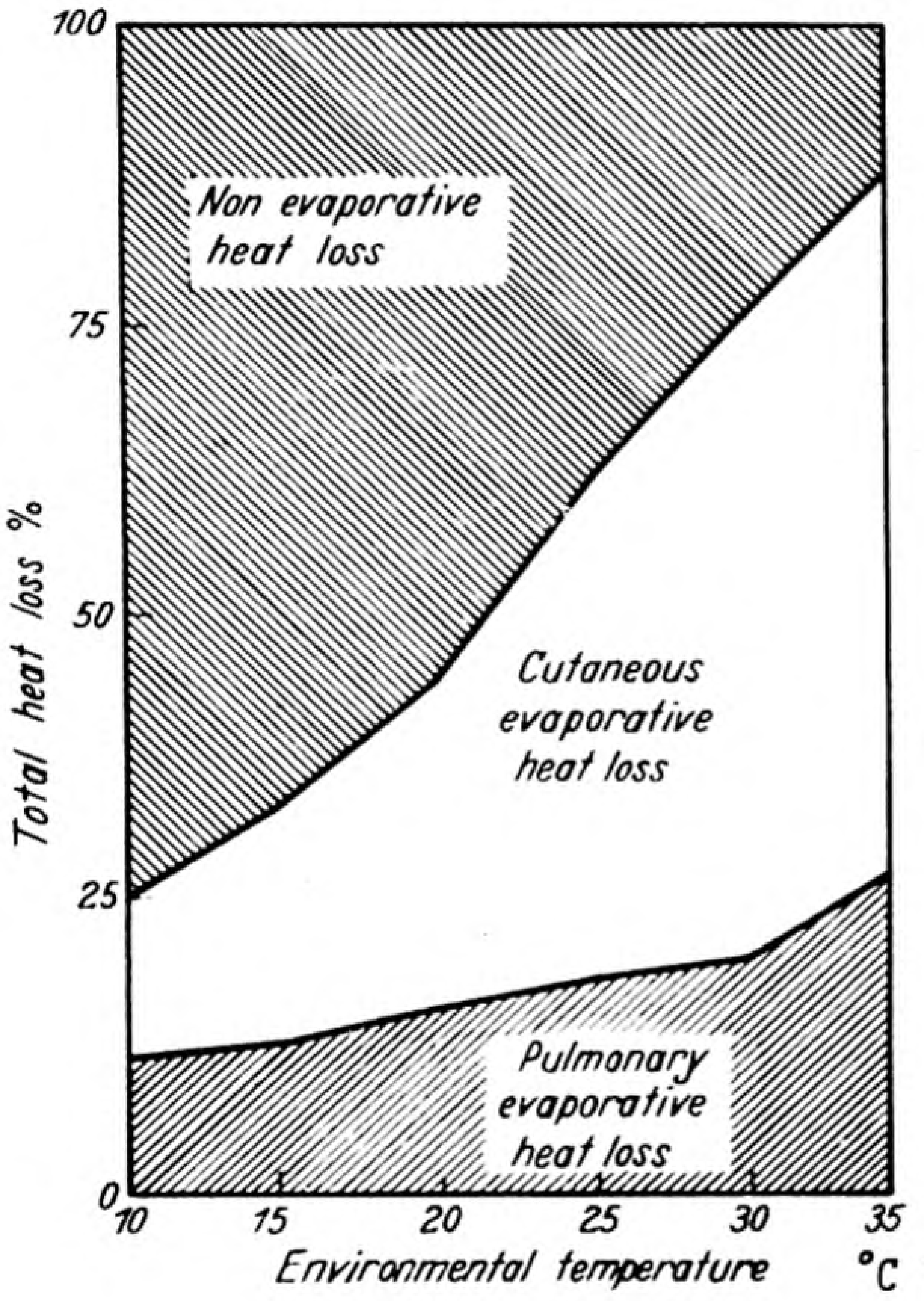


Figure 6.19. The partition of evaporative and non-evaporative heat loss in the bovine (from Kibler and Brody, 1950b, by courtesy *Res. Bull. Mo. Agric. Exp. Stn.*).

It might be thought that the sudden rise in surface vaporization rate in the cow above 65°F. was analogous to an ‘ outbreak of sweating ’ in man. Quantitatively, however, the difference in sweating or skin surface vaporization rate between the cow and man on the basis of the figures given by Brody *et al* is very great. A man in dry air can sweat at the rate of approximately 24 g. per kg. body-weight per hour (ADOLPH, 1938, 1946; ADOLPH and DILL, 1938), whereas the cows cited in these studies could attain a maximal vaporization rate of only 1·5 g. per kg. body-weight per hour.

Many workers have made measurements of the skin temperatures of cattle and to a limited extent of sheep and swine. The work (*see*

FINDLAY, 1950) has shown that the skin temperature of cattle increases by about 0·3°F. for every 1°F. rise in air temperature.

The thermal gradients between the skin, the tips of the hairs of the coat and the environmental air have lately been investigated in cattle by THOMPSON, WORSTELL and BRODY (1951, 1952). The thermal conductances of the two media have been calculated from these gradients together with the non-evaporative heat loss from the animals. It has been shown that there is a very large temperature drop between the tips of the hairs and the environment and that this drop is greater than that between the skin and the tips of the hairs for environmental temperatures of 0° to 100°F. At 100°F. the temperatures of the skin, the tips of the hairs and the environment become virtually the same.

No significant differences in these relationships have been observed between Brahman and European type cattle. All the experiments have been performed in still air and there are no experiments extant on the effect of air movement on cattle.

No work of a similar nature to that given for cattle has appeared in the literature for sheep or swine and little is known of the quantitative aspects of heat loss from these animals. Work on sheep by RIECK *et al* (1950) to be discussed later (page 293) in another connection has indicated that about 20 g. water per hour are insensibly perspired by the sheep. Water losses in hot atmospheres observed by these workers cannot be accounted for solely by insensible perspiration and vaporization loss from the respiratory tract. This would appear to indicate a functional sweating ability in the sheep, but such a view must be reserved till the publication of more extensive and detailed work on the subject.

The present state of knowledge on the quantitative aspects of heat loss from farm animals still appears to classify them as slightly-sweating species of mammalia, but much more work is necessary before even tentative numerical assessments can be made.

HEAT REGULATION AND THE PLANE OF NUTRITION

The question has often been posed as to whether heavy feeding renders animals unsuitable for tropical conditions, *i.e.* whether the plane of nutrition affects heat regulation in animals.

It has for long been known (BENEDICT and RITZMAN, 1923) that the plane of nutrition affects the skin temperature of steers in that within certain limits skin temperature increases as the plane of nutrition improves. This would not be an advantage to animals in a hot climate. Other work has suggested that low skin temperatures are associated with high live-weight gains but this has been seriously contested (LEITCH and THOMPSON, 1944).

A change in the intake of food should affect heat production and in conditions in which heat loss is rendered difficult by the environmental conditions, the heat regulation of an animal should be put under stress in maintaining the heat balance. The plane of nutrition would, in fact, affect the left hand side of the heat balance diagram in *Figure 6.1* and would thus also affect the amount of heat to be lost.

The exact quantitative assessment of the effect of plane of nutrition on the heat balance of farm animals has received scant attention. ROBINSON and LEE (1947) have studied in some detail the effect of plane of nutrition on the general physiological reactions of sows and sheep exposed to hot atmospheres for 7 hours once per week in a psychrometric room. The animals were alternately exposed week by week to hot-wet (D.B. 85°F.; W.B. 84°F.) and to hot-dry (D.B. 105°F.; W.B. 87°F.) atmospheres and their cardiorespiratory and rectal temperature behaviour noted and their weight gains recorded. The animals were used in groups of four, two of which were fed only maintenance rations while the other two were given free access to adequate food mixtures.

With the sows, which were of the Middle White breed, it was shown that the high-plane diet resulted in highly significant rises in rectal temperature, respiratory rate and weight loss in the hot atmospheres compared with the sows on the low-plane diet. The differences were not greater in the hot-wet than in the hot-dry atmospheres. Rises in the pulse rate were also significant, though not so marked. The reactions of the sows were also measured previous to exposure in an ante-room at normal temperature and humidity, and here also the high plane diet produced significant rises of rectal temperature, pulse and respiration rate, though of less magnitude than those occurring in the psychrometric room.

Similar results were obtained for 8-month old Border Leicester-Merino cross wethers in identical experiments, except that the increases brought about in rectal temperature and pulse rate were no greater in the hot atmospheres than in the ante-room. The increase in the respiratory rates were, however, much greater in the hot atmospheres than in normal ante-room temperatures. Reversal of the diets reversed the trend of the hot room reactions after a few days. These effects are shown in *Figure 6.20* redrawn from the data of ROBINSON and LEE by the present authors.

Theoretical deductions from demonstrations of the specific dynamic effect of protein have led to the belief that high protein diets are not of advantage to animals exposed to heat stress. Robinson and Lee have attempted to assess the effect of the proportion of protein in iso-caloric diets on the reaction to heat stress of sows and sheep. Three basic food mixtures were used out of which five iso-caloric rations were made up containing from 5 per cent to 28 per cent of protein. The calorific value of the ration amounted to 1,600 g. cal. per lb. The ration given to the sheep and sows was 3 lb. per day. The animals were fed for a week on each of the five rations in succession and exposed to a hot atmosphere of D.B. 106°F. and W.B. 82°F. and their physiological reactions measured. It was found that the proportion of protein in the diet had no effect whatever on the physiological reactions of the animals to high temperatures and therefore did not appear to affect their heat regulation. This is in conformity with the results found for man by PITTS, CONSOLAZIO and JOHNSON (1944).

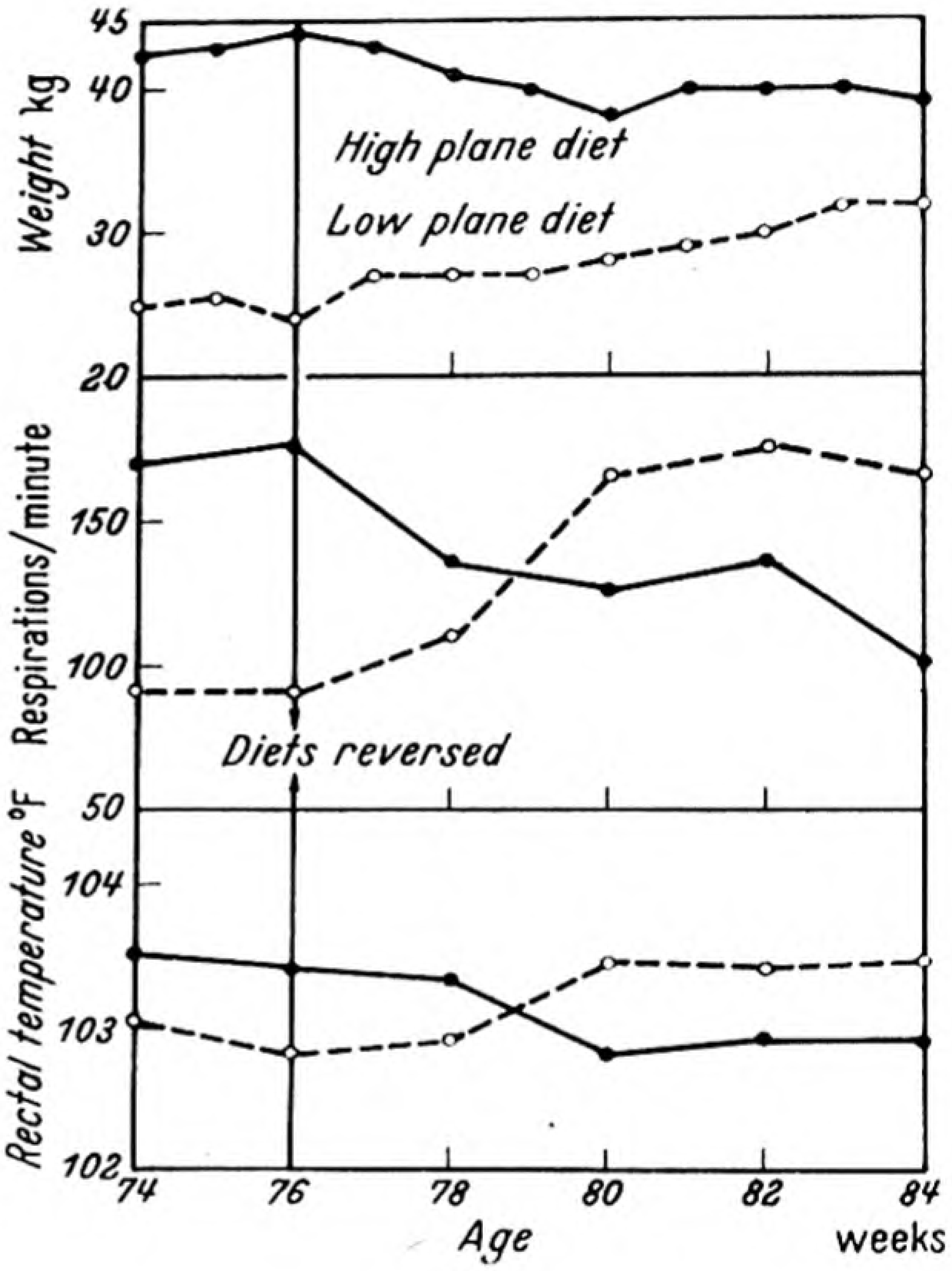


Figure 6.20. The effect of plane of nutrition on the weight gain, respiration rate and rectal temperature behaviour of sheep exposed to high temperatures (from Robinson and Lee, 1947, by courtesy *J. Anim. Sci.*).

RIECK *et al* (1950) have extended these experiments on the effect of dietary plane on the reactions of sheep by studying in detail the reaction of two breeds of sheep—Camden Park Merinos and Corriedales—to hot atmospheres ranging from 86° to 113°F. at vapour pressures from 15 to 40 mm. Hg. when the sheep were fed at high, medium and low dietary levels. It was found that of the two breeds of sheep, the Merinos were the most tolerant of high temperatures as judged by their rectal temperature and cardiorespiratory behaviour. A high plane of nutrition was shown to reduce the heat tolerance of the sheep, some heavy individuals actually losing weight during experimental periods. On the other hand, the experiments also showed that a very low-plane diet also impaired heat regulation probably because of a general depression of functional response. Those sheep on a medium plane of nutrition were the most tolerant and showed least upset in their heat regulation and ability to withstand thermal stress. It may be tentatively concluded from such experiments that starvation would impair heat regulation not only against cold but also against heat and that although in starvation the metabolic rate would be reduced this advantage in hot conditions would probably be offset by the general effect of starvation on the neuro-endocrinological systems of the animal with consequent impairment to heat loss mechanisms.

It is to be noted that, unlike other aspects of heat regulation the effect of plane of nutrition has not been studied in cattle as it has in sheep and pigs. Extensive experiments on this aspect with cattle would be of great value in solving problems concerned with the tropical feeding of cattle and would give valuable information on the proportion of protein to carbohydrate that could be maintained in their diet without adversely affecting their toleration of high temperatures.

CONCLUSION

From the studies dealt with in this chapter it will be apparent that very little is yet known of the fundamental physiology of temperature regulation in cattle and other farm animals. Knowledge of the innervation and endocrinological relations of the so-called sweat glands of cattle, sheep and pigs, is still lacking. The mechanism of the transudation of water through the hides and the investigation of water-restraining barrier layers and the ways in which they function are, as yet, largely unknown. Although the anatomy of the vascular supply to the skin of cattle has lately been elucidated for the first time, nothing comparable is known for sheep or pigs. Since much heat is lost through the skin, knowledge of peripheral blood flow in farm animals would greatly help towards an understanding of the mechanisms of heat regulation.

The quantitative aspects of heat loss from farm animals require detailed and prolonged study and, although attempts by various workers to partition the various channels of heat loss and particularly the extent of vaporization loss between the skin and respiratory passages, have appeared in recent years, the numerical specification of the various heat loss channels remain largely conjectural.

A conspicuous gap in the knowledge is apparent in relation to the effects of environmental conditions on the neuro-endocrinological systems of farm animals. The part played by the thyroid and adrenal glands particularly requires much investigation in relation to the mechanism of heat regulation.

Fundamental to all these studies must be an expansion of knowledge concerning the central cortical regulation of temperature in mammalia and the nature of peripheral temperature receptors. Such an expansion must await the development of more advanced techniques and instruments than are available at present.

Nevertheless, from studies made in recent years some knowledge of practical value to the animal husbandryman and the veterinarian has emerged. The optimal environmental temperature for milk production in cattle appears to lie about 60°F. and from data for cattle on heat production and moisture vaporization in relation to environmental temperature the architect of farm byres should be considerably helped in designing for the maintenance of this optimal temperature so putting the construction of byres, for the first time, on a physiological as opposed to an empirical, basis. It also appears that cattle sweat but slightly, so that their comfort cannot be judged by human standards of ventilation. Similar data, though of a more tentative nature is available for swine and ameliorative measures to guard against the effects of high temperatures on swine have been suggested. The amelioration of conditions for cattle in the tropics may be enhanced by proper design of tropical shelters and by such treatments as water sprinkling, with consequent good effects on production.

Economically, however, it is in the field of the comparative heat tolerance of animals that the greatest gains are likely to be made. Research on the heat regulation of various breeds of cattle under psychrometric laboratory conditions should one day result in the devising of physiological tests of comparative thermal ability and such tests translated by field workers into terms of productive capacity should give the tropical breeder a ready means of selecting breeds and individuals suitable for specified climatic conditions. In discussing the question of the comparative heat tolerance of animals it must be made clear that any physiological measurement of reaction to heat stress can be related to heat tolerance only if it is first related to productivity since the latter factor is the ultimate end of all such work on farm animals. It follows from this that any attempts to draw up scales of comparative reaction to thermal stress comparable to the effective temperature scale widely used in human environmental physiology, must be related to the economic purpose of farm animals, their productivity.

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CHAPTER 7

HEAT REGULATION IN BIRDS

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THE MAIN subject of this chapter is the heat regulation of agricultural birds. Of these the fowl alone has been studied in any detail, so that only brief reference is possible to ducks, geese and turkeys. Thermoregulation in the fowl can, however, be illuminated by comparison with wild birds. Indeed, there are some aspects of the subject on which information on wild birds only is available. In addition, it is instructive to make some comparisons with mammals and poikilotherms. Of the mammals man here is the most important, because a good deal is known about his heat regulation, and because the fowl and man live in close association.

To remain at a temperature which will support life an animal, whether it is a homeotherm or a poikilotherm, must dissipate its metabolic heat by conduction, convection, radiation and evaporation of moisture. In poikilotherms the evaporation of moisture is normally sufficient or more than sufficient to dissipate the heat. Consequently, when shielded from radiation, and resting, they exhibit a body temperature close to or below that of the environment. Homeotherms, on the other hand, have a higher metabolic rate, which is also higher than the normal rate of evaporative cooling, and are covered with a heat insulating layer of fat and hair or feathers. Consequently, their body temperature is in most circumstances above that of the air, and the brain and contents of the body cavity are maintained at a constant temperature, though there is considerable variation in that of the limbs and appendages in different environments. In this chapter when ‘ body temperature ’ is mentioned, it is the central temperature that is meant, not that of the extremities. To maintain the central temperature constant birds are provided with physiological mechanisms for regulating the production and dissipation of heat. In this chapter such physiological regulation is called endothermic control.* Both homeotherms and poikilotherms can also regulate their body temperature by adapting their behaviour to the thermal situation. This is called ectothermic control. Homeothermy in birds probably developed later than in mammals, and its evolution was certainly independent. It is not remarkable that two types of animals should have found it advantageous to control deep body temperature accurately by powerful endothermic methods ; but the similarity of the physiological mechanisms involved is a striking case of parallel evolution. Birds occupy many of the biological niches formerly inhabited by pterosaurs, which are supposed to have been poikilotherms.

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* COWLES (1940) suggests the name endotherm for homeotherm, and ectotherm for poikilotherm, because both types of animal can regulate their body temperature, and the difference between them is chiefly in the methods by which this is accomplished.

BODY TEMPERATURE OF ADULT BIRDS

Table 7.1 shows the normal day-time temperature of the different classes of homeotherms. Since there are large differences between species within classes and the temperature of some animals is variable, the figures are very rough. They show clearly, however, that the later evolved mammalian types have the higher body temperature, but that birds, which evolved before eutheria and marsupials have the highest of all. Although homeotherms can maintain their central temperature stable in a wide variety of climates it does, nevertheless, vary from time to time, and much of this variation is due to the state of activity of the animal. Thus the rectal temperature of eastern house wrens is never less than 108°F. on capture, but with the birds completely quiet at the end of a 4–5 hr. fast it is 104–105°F. (Baldwin and Kendeigh, 1932). Similarly, the temperature of fowls usually falls when they are put in small cages in a climatic chamber at an equable temperature under conditions in which they are bored and inactive. The fall takes place in the first hour before the crop has time to empty. In man it has been found that the body temperature rises with exercise under conditions well within the capacity of the thermo-regulatory system (Nielsen, 1938), so the normal body temperature of man, like birds, is affected by activity.

Table 7.1

NORMAL BODY TEMPERATURE OF DIFFERENT TYPES OF HOMEOTHERMS

Type	*Body temp.* (°*F.*)	*Authority*
Monotremes	85 (variable)	Martin (1903); Robinson & Lee (1946)
Marsupials	93–98	Martin (1903); Robinson & Lee (1946)
Eutheria (excluding Xenarthra)	98–103	Wislocki (1933)
Families of birds	104–109	Wetmore (1921)
Fowl	106–107	Fronda (1921); Robinson & Lee (1946)
Duck	106	Robinson & Lee (1946)
Goose	105	Fronda (1921); Benedict & Lee (1937)
Turkey	106	Fronda (1921); Robinson & Lee (1946)

The body temperature rises after ingestion of food, and is higher in animals maintained on a high plane of nutrition (Robinson and

LEE, 1947). As would be expected from the effects of activity and food, there is a diurnal rhythm of body temperature, which is illustrated in *Figures 7.1* and *7.2*. This rhythm is normally independent of the diurnal rhythm of environmental temperature. Thus, in nocturnal birds, such as owls, the body temperature is highest during the night, when the environmental temperature is at its lowest. HILDÉN and STENBÄCK (1916) were able to reverse the diurnal rhythm of body temperature by reversing the light cycle, without reversing the cycle of air temperature.

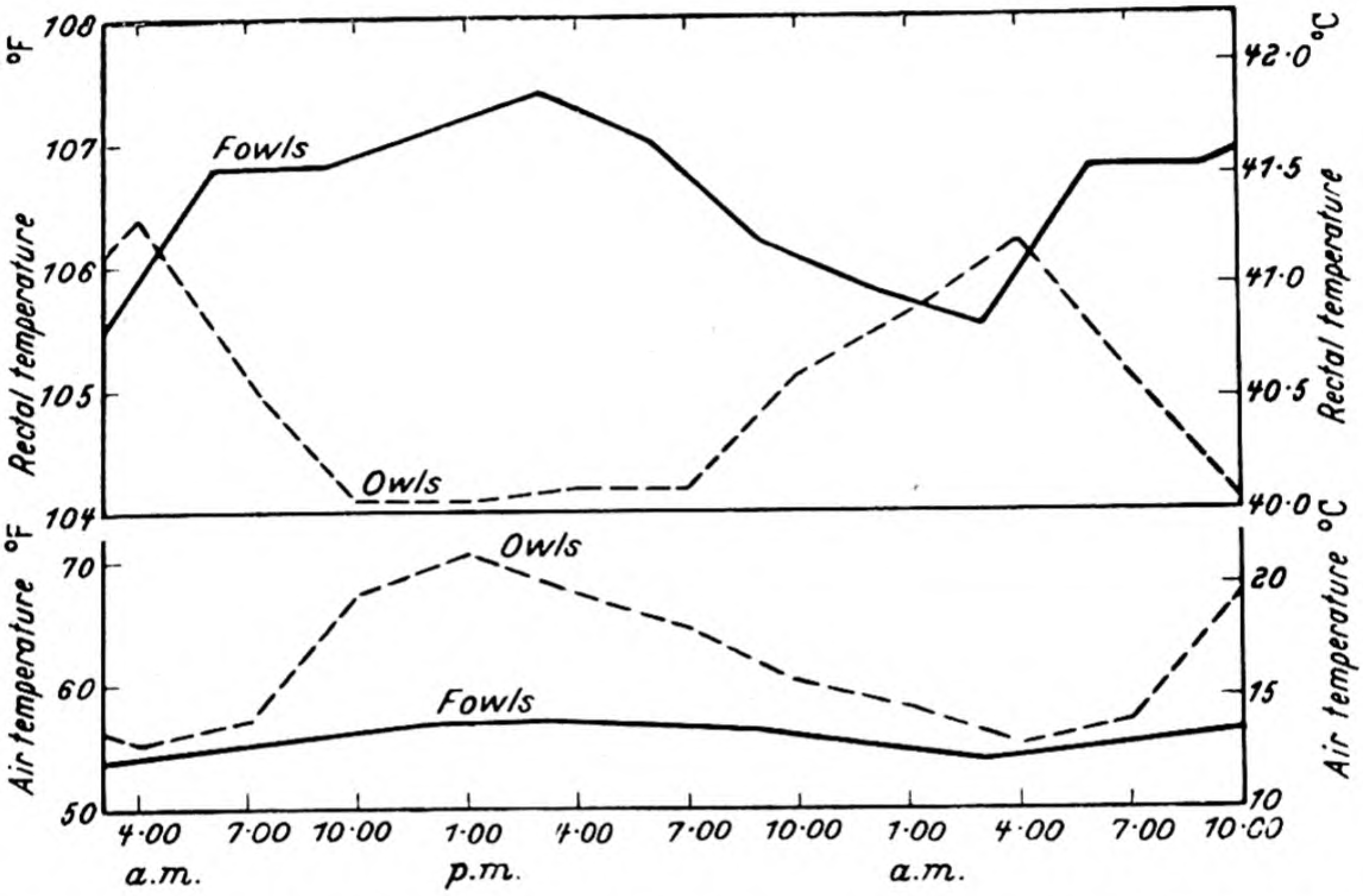


Figure 7.1. Diurnal rhythm of body temperature in fowls and owls. Average for 2 Dorking fowls and 3 owls over a number of days in summer. There was an adequate preliminary period to accustom the birds to the observations. (Data extracted from Simpson and Galbraith, 1905.)

When the air temperature is close to that of the skin, the greater part of the metabolic heat must be dissipated by evaporation, and when the atmosphere is hotter than the skin, all the metabolic heat plus the heat which leaks into the animal from the environment must be so dissipated. This state of affairs is not often encountered by birds owing to their high body temperature. But they are not on this account ill adapted to cold climates; in fact, the necessary physiological reactions to a change in climate are less than are required for animals with lower body temperature. A simple calculation will illustrate this point, and to make it more intelligible evaporative cooling will be neglected, an omission which does not seriously affect the argument. An echidna with a body temperature of 85°F. in an environment of 70°F. has a temperature difference between its body and its surroundings of 15°F. Its heat loss by convection, conduction and radiation is roughly proportional to this gradient. Therefore, if it moves into an environment of 55°F. its heat loss will be doubled because the gradient is doubled. It must, therefore, either increase its metabolism or its effective heat insulation by 100 per cent if it wants to maintain homeothermy. By contrast, a fowl with a normal body temperature of 106°F. has a gradient of 36°F. at an environmental temperature of 70°F. At 55°F. ambient temperature this would become 51°F. To maintain homeothermy it, therefore, only has to increase its metabolism or effective insulation by about 40 per cent. In practice heat regulation in echidna is very poor, and this is no doubt partly due to the low body temperature.

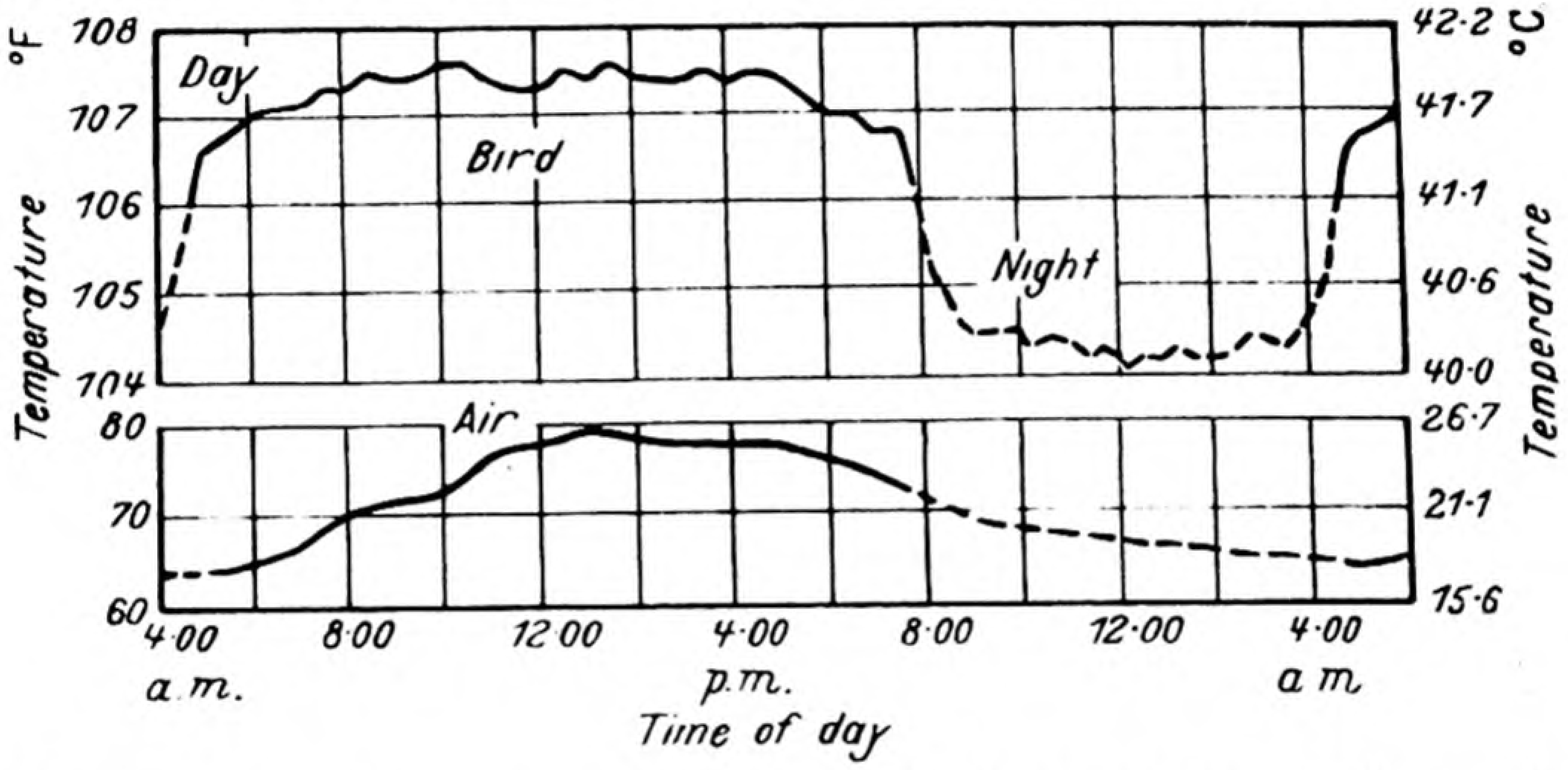


Figure 7.2. Average daily rhythm in body temperature of passeriforme birds. These records comprise 8 species, 12 individuals and 75 days, correlated with air temperature, and show the effect of activity during the day (continuous line) against the quiet at night (broken line). The body temperature was automatically recorded during periods when the birds were sitting on their nests, so that real natural conditions only are represented. The large diurnal rhythm in comparison with man is more probably due to the flighty day-time behaviour of birds than to a difference in their system of heat regulation. (From Baldwin and Kendeigh, 1932, by courtesy *Sci. Publ. Cleveland Mus. Nat. Hist.*)

The body temperatures of birds are not adapted to the particular climates in which they live. For example, that of Antarctic species is not lower than for species living in the tropics (EKLUND, 1942). It has, however, been reported that the Lapland tit (*Parus cinctus*), the most northern member of this family of very small birds, has a somewhat low body temperature, but this is an exception (PALMGREN, 1944).

HEAT REGULATION IN ADULT BIRDS

ENDOTHERMIC CONTROL

Nervous control of body temperature

The centres for heat regulation in homeotherms are described by MARTIN (1930). For birds VON SAALFELD (1936) found a centre located in the mid-brain which is sensitive to changes in blood temperature, and can initiate polypnoea to increase evaporative cooling. The rate of respiration appears to depend on the central temperature, not on reflexes from the skin. At a given rectal temperature it is the same whether the temperature is rising or falling, unless the change is exceedingly rapid (RANDALL and HIESTAND, 1939; RANDALL, 1943). In dogs thermal polypnoea can be induced by a conditioned reflex (HAMMOUDA, 1933), but this does not happen in fowls (HUTCHINSON, unpublished observations). Shivering, on the other hand, can be elicited by skin reflexes as well as by central cooling (Randall, 1943).

Insulation

Anatomical structures which hinder the loss of heat in birds are subcutaneous fat, which can increase the thermal insulation of the tissues, and feathers which, by creating a layer of still air round the body, provide the greater part of the thermal insulation. It is the presence of the insulation and their high metabolism which enable homeotherms to maintain a body temperature, which is usually much higher than that of the environment.

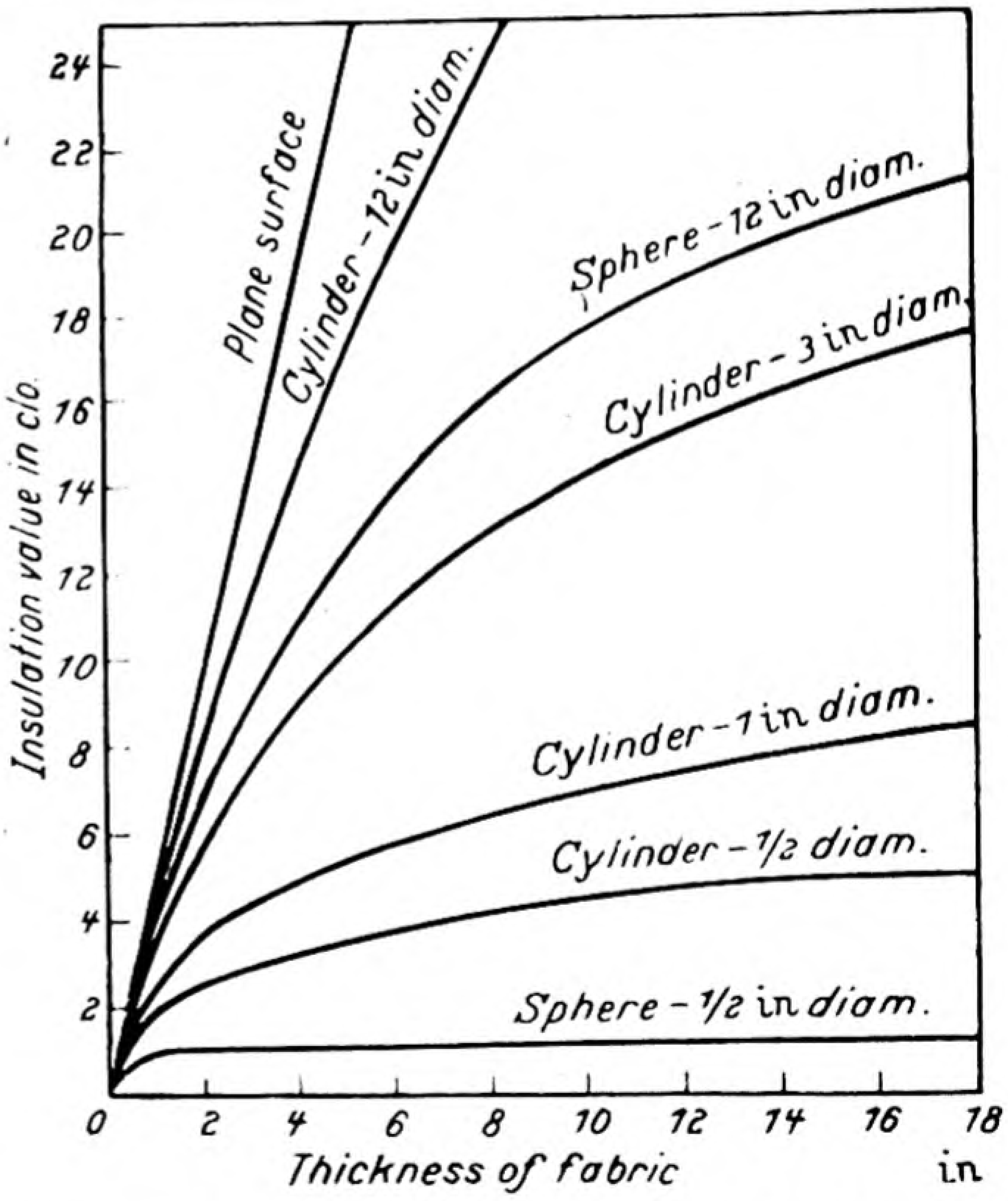
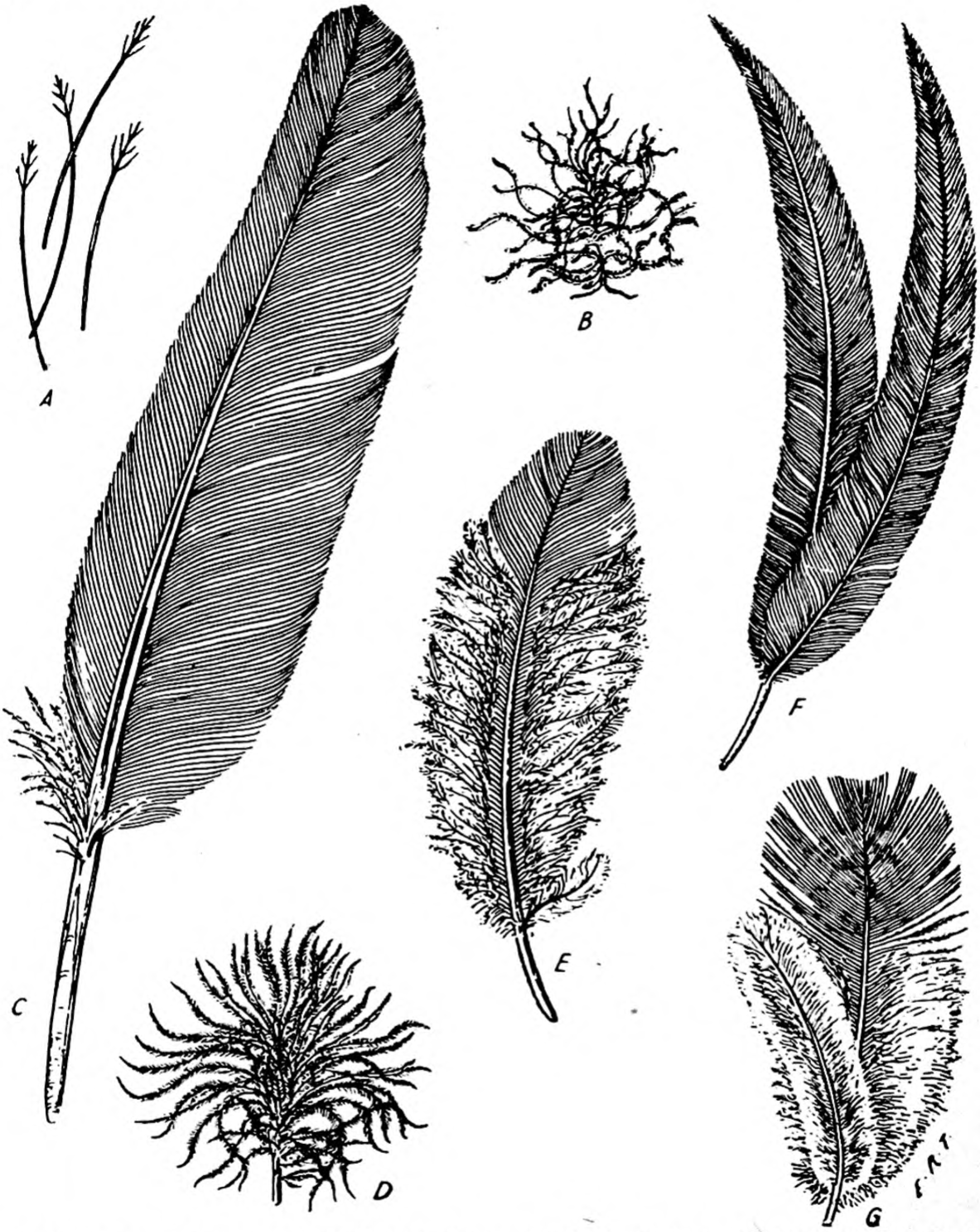


Figure 7.3. Effect of curvature on insulation of an 'ideal' fabric. 1 clo of insulation is roughly equivalent to a suit of battledress. (From van Dilla, Day and Siple, 1949, by courtesy, Saunders.)

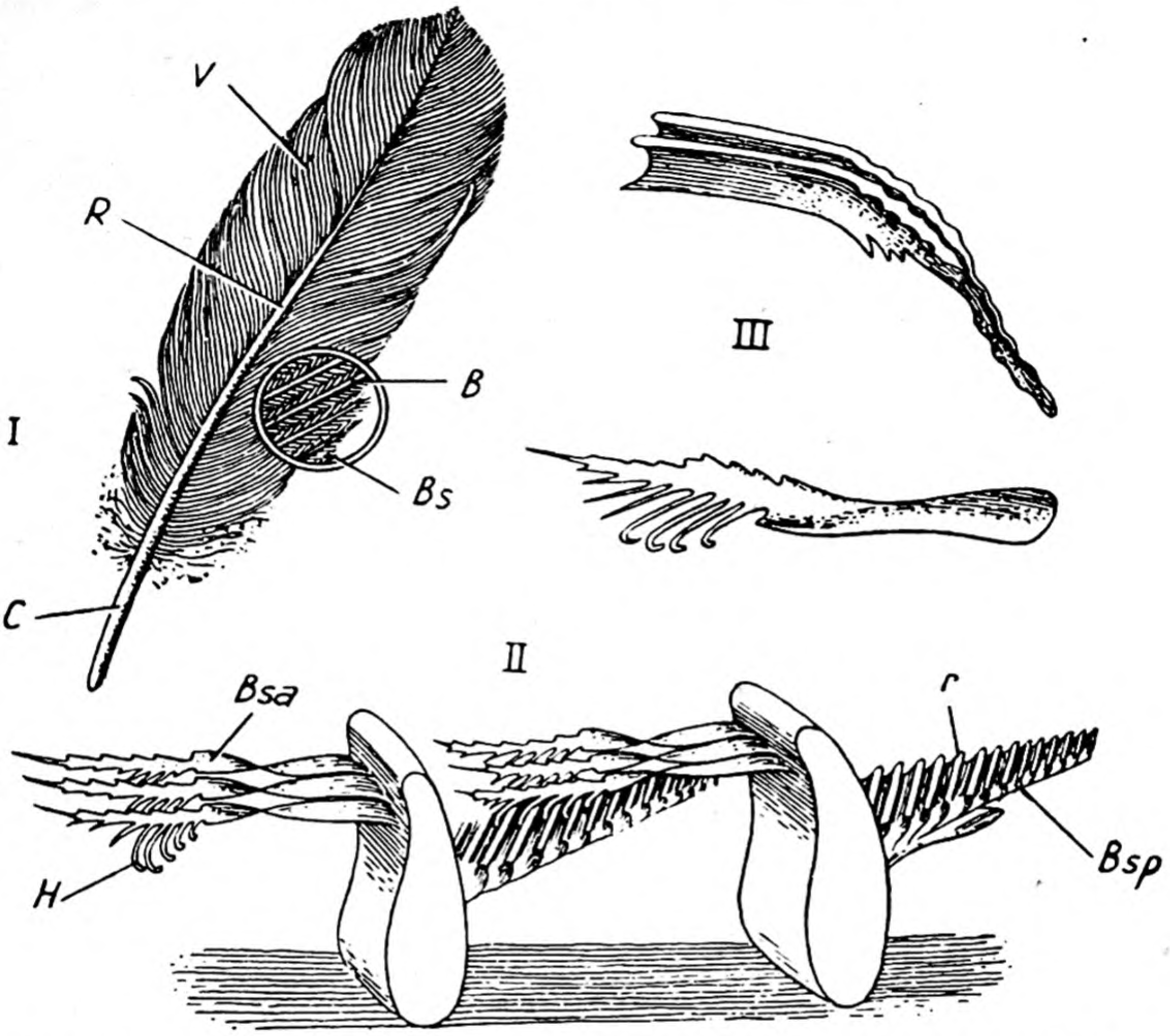
The insulating value of clothing depends on the shape of the clothed object as well as the nature and thickness of the material. The value per unit thickness is less when fixed to a convex than to a plane surface. This effect of curvature is illustrated in *Figure 7.3.* The radius of the neck of a fowl is small enough for the insulating value of the feathers to be appreciably affected by the curvature. Similarly, the radius of a wren's body is well within the limits where curvature is important. Probably one of the reasons why the narrow legs of most birds carry no feathers is because feather insulation would save very little heat loss.



A, filoplumes; *B*, nestling down feather; *C*, primary wing feather of pigeon; *D*, permanent down feather; *E*, feather with free barbs; *F*, emu's feather with long aftershaft; *G*, contour feather of pheasant with aftershaft.

Figure 7.4. Various types of feather. (From Young, 1950 ; partly after Thomson, 1923, by courtesy Clarendon.)

Subcutaneous fat.—In most birds the fat is mainly abdominal and, therefore, plays little part in temperature regulation. This is the case in the fowl, and in this respect it is different from most agricultural mammals. There are, however, many wild birds which carry fat under the skin. For instance, penguins carry a heavy layer of blubber, whilst sea ducks and petrels contain enough subcutaneous fat to aid thermal insulation. Even the domestic duck and goose have more subcutaneous fat than the fowl or turkey.



I. Whole feather showing calamus (quill), *C*; rhachis (shaft), *R*; and vane, *V*. On the right side a small area is shown as it appears under a lens; *B*, barb; *Bs*, barbule. II. A section cut at right angles to two barbs in the plane of the barbules of the anterior series (*Bsa*). Note how the hamuli, *H*, of the anterior barbs interlock with ridges (*r*) on the posterior barbules (*Bsp*). III. Shows one anterior and two posterior barbules isolated.

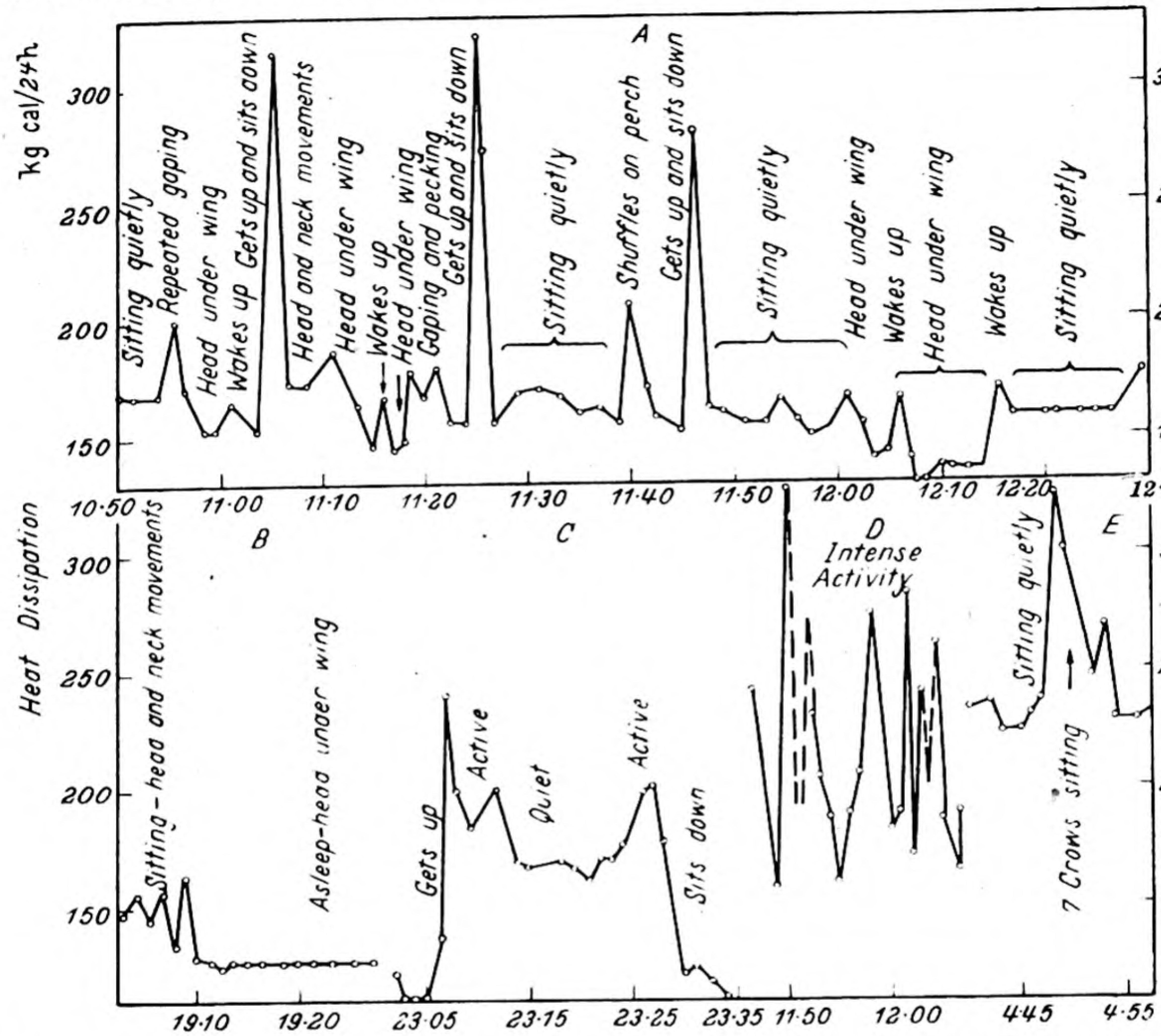
Figure 7.5. The structure of a flight feather. (From Young, 1950; after Pycraft, 1910, by courtesy Clarendon.)

Feathers.—The well known experiments of Benedict, Landauer and Fox (1932) on the frizzle fowl illustrate the essential role of feathers in maintaining homeothermy. Their structure is shown in *Figures 7.4* and *7.5*. The down feathers are admirably designed to stabilize a maximum volume of air with a minimum weight of feathers (*Figure 7.4*, *B*, *D*). Anyone who has used an eiderdown sleeping bag will appreciate how successfully this combination of lightness and high insulation is achieved. The contour feathers (*Figure 7.4*, *E*, *G*) have the insulating properties of down feathers in their lower half or two-thirds, while the tips are flat owing to interlocking of the barbules as shown in *Figure 7.5*. They curve over the down underneath giving an outer windproof layer to the bird's clothing. This is the principle of most arctic 'clothing assemblies' used by man, that is layers of insulation covered by a thin outer windproof shell. The direction of the contour feathers is for the most part pointing backwards, so that a bird should be more windproof if it faces the wind. The rachis of the contour feathers gives the clothing assembly some rigidity to compression without interfering with the movements of the bird. In the covering of birds, unlike that of man, there is little risk of condensation of moisture in the outer layers from insensible perspiration, for birds can at any time make their feathers ventile by shaking themselves. The flight feathers (*Figures 7.4, C,* and *7.5*) are flat, and windproof, to perform their functions in flight. The ' clothing assembly ' of birds is more highly specialized than the fur of mammals which consists of a guard layer of coarse hairs covering an inner coat of fine ones.

The insulating value per unit thickness of feathers is high and comparable with the best clothing materials. Indeed, a dead air cell loosely filled with eiderdown has a higher insulation than still air, because the small fibres interfere with radiation as well as with convective air currents (SIPLE, 1949). The insulation of different species of birds depends mainly on the depth of feathering. In cold climates, therefore, the small birds are under a disadvantage because they can carry less plumage without restriction of movement and also on account of their curvature mentioned above. SCHOLANDER and his colleagues (1950a) have shown that insulation in arctic mammals is only independent of body size for creatures larger than the arctic fox. There must also be a critical body size in birds.

If the heat dissipation of a fowl is continuously measured, it is found to vary rather suddenly from minute to minute except when the bird is quite motionless, as for example when it sleeps with its head under its wing. *Figure 7.6* shows the heat dissipation of Light Sussex cocks. It may be seen that when the birds become active there is an immediate dissipation of more heat. This is not just due to the greater heat production of exercise, for it could easily be shown that, if it were so, the skin temperature would have to rise suddenly to an impossible height. What happens is that when the feathers are disturbed the hot air entrapped is suddenly released, and this release of stabilized air is equivalent to a sudden reduction of insulation. Also the changes in posture may expose a greater effective surface for heat dissipation. Consequently activities which involve little exercise but some disturbance of the feathers, such as shuffling on a perch, cause a large evolution of heat as well as those which involve more strenuous work (DEIGHTON and HUTCHINSON, 1940). This ' bellows action ' of the clothing is a means of dissipating the heat of work. It takes place even before the heat of recovery of the muscles is produced, and probably before the heat of contraction reaches the skin, thus anticipating the need for increased heat dissipation. The insulation of human clothing is likewise reduced during physical work (Belding and his colleagues, 1947).

The heat insulation of birds can be adjusted by fluffing out or flattening the feathers, thus altering the depth of insulation. Kendeigh's house wrens (Baldwin and Kendeigh, 1932 ; Kendeigh, 1939) could tolerate a temperature only of 50°F. when lack of space prevented complete fluffing. They could endure 26°F. with a little more space, so feather erection has a considerable effect on cold tolerance.



A, continuous record of a test showing effect of various activities; *B*, part of a test showing how steady the dissipation can be, when the bird is motionless with its head under its wing; *C*, period of continuous standing; *D*, intense activity. During the 20 min. charted the bird stood up and sat down 7 times, flapped its wings 6 times, shuffled on the perch 4 times, and engaged in vigorous preening for most of the remainder of the period. This activity may seem excessive to a calorimetrician, and, in fact, defeated the observers, but it is quite normal for a cock in ordinary life. *E*, effect of crowing. This bird was fed; the others fasted. Abscissae time on 24-hour system.

Figure 7.6. Rapid changes in heat dissipation of Light Sussex cocks in a Noyons direct calorimeter (evaporation included). The birds sat or stood on a perch 1½ in. wide. Ambient temperature ranged from 79·5° to 83·3°F. in different tests; mean radiant temperature close to air temperature; air movement high and turbulent, of the order of 200 ft./min. The peaks of heat dissipation were too sudden to be registered exactly by the calorimeter. The rapid changes may be less marked at low air movement. (From unpublished observations of Deighton and Hutchinson.)

In fowls there are breed differences in the closeness of the plumage. Thus, Leghorns and Jungle Fowl have a close plumage, while that of

Rhode Island Reds is more open but thicker. Consequently, the insulation of Rhode Island Reds should be the greater in still air. The thickness of feather insulation of a Brown Leghorn cock and hen in the author's laboratory averaged roughly 2 cm. in an environmental temperature of 60°F. If the insulation per unit thickness is much the same as that of human clothing and mammalian fur, the clothing of the fowl has very roughly 2–3 times the insulating value of a suit of battledress,* so fowls are well clothed. This is a very rough estimate, because the insulation may be adjusted to requirements. The plumage of ducks and geese is closer than that of fowls and turkeys and, therefore, should be more windproof.

Many birds spend a good part of their lives swimming, yet their feathers do not become waterlogged. The principle of the waterproof properties is the same as that of a kapok life jacket. The spaces between the feathers are small, and a layer of oil secreted by the preen gland makes them water repellent. Capillary action prevents the water rising through the spaces, just as the meniscus is depressed in a fine glass tube inserted vertically in a bath of mercury. The water pressure which plumage can repel has not yet been measured, but those familiar with the difficulty of designing kapok life jackets will appreciate the efficient arrangements evolved in water birds. Of course, birds owing to their shallow draught are not called upon to repel a large water pressure; for even in diving it is only the difference in pressure just above and just below the bird that the capillary action must work against. The air entrapped in the submerged part of the feathers not only provides buoyancy, but maintains the thermal insulation between the bird and the water. For this latter purpose man must wear a cumbersome immersion suit, or provide himself with a boat. Of the mammals the water shrew can swim under water without its coat becoming sodden (LORENZ, 1952), while some others can maintain the undercoats dry. The polar bear and seal, by contrast, lose the insulation of their coats when they swim (Scholander *et al*, 1950a).

Energy metabolism

A detailed account of the complexities of energy metabolism is beyond the scope of this chapter, but the subject is discussed at length by BENEDICT (1938), BRODY (1945) and KLEIBER (1947). Two questions only will be examined here, first whether basal metabolism is adapted to the needs of heat regulation, and secondly how far the metabolism exhibited in ordinary life is so adjusted.

Basal metabolism and climate.—It might be expected that species normally living in cold environments would have a higher basal metabolism than those residing in more equitable situations. There is some evidence for this, because values for arctic gulls and penguins are high (Scholander, 1940; Scholander *et al*, 1950c). On the other hand, the figure for snow buntings is about average. More work will be required to settle this important point, especially in view of the known effect of physiological acclimatization (page 321).

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* 1 in. thickness is reckoned to provide 4 clo units of insulation (FOURT and HARRIS, 1949). The insulation of a suit of battledress without underclothes is counted as 1 clo on the basis of unpublished measurements by Professor A. C. Burton.

Basal metabolism and body size.—Rubner (1883) by his great surface area law,* drew attention to the connexion between the energy metabolism of homeotherms and their requirement of heat to maintain a body temperature above that of the surroundings. He argued that the amount of sensible heat† dissipated was proportional to the surface area, and found that this was roughly true also for basal metabolism. The heat dissipation, however, depends on the heat insulation as well as the surface area, and small animals can carry less effective insulation than large ones (page 306); so the basal metabolism per unit area of small species of birds should be higher, if it were adapted to their homeothermic needs. In fact, the basal metabolism of birds varies as the 2/3 power of the body weight, as if the value per unit area were roughly constant (Brody, 1945), whilst in mammals it varies as the 0·73 power. Moreover, it is an interesting fact that the basal metabolism of reptile species follows the surface area law more closely than that of mammals (Benedict, 1938), though in their case it cannot have much relation to temperature regulation (*see* page 299) except, perhaps, in large dinosaurs. Nevertheless, basal metabolism is better adjusted for thermo-regulation than if it were proportional to body weight. For example, Kleiber (1947) calculates that ‘ a 60 g. mouse, with the same metabolic rate per unit weight as a steer, would need the equivalent of a steer's surface covering in a 20 cm. thick layer to maintain its body temperature in an environment of 37°F.’ With this encumbrance the mouse, even if it could move at all, would be a sitting target for a cat.

In examining the relation between basal metabolism and body size it is tacitly assumed that the basal metabolism is a standard one for all species; otherwise there would be no sense in making interspecific comparisons. It seems very doubtful if this is so for all sizes of birds. Many of the smaller species can only tolerate starvation for a day or two even when resting quietly in the dark in an equable environment (Kendeigh, 1945). Consequently, when a small bird reaches the post-absorptive state necessary for the determination of basal metabolism, it is pretty near to death from inanition. On the other hand, the domestic goose can fast for a month or so without ill effects (Benedict and Lee, 1937). Its metabolism per unit area decreases considerably during this time, and there seems no reason why one should take as basal the metabolism after a 24- or 48-hr. period of starvation, as is customary, rather than that exhibited after a fast of some weeks. If basal metabolism for different sizes of birds is not the same thing, it is hardly surprising that its relation to heat regulation is a vague one.

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* First formulated by Sarrus and Rameaux (1839).

† Sensible heat means heat dissipated by convection, conduction and radiation as opposed to that lost by evaporation of moisture.

Metabolism exhibited and thermo-regulation.—Whatever the basal metabolism, the rate actually exhibited in ordinary life is, in cold environments, pretty closely adjusted to the needs of heat regulation. The temperature difference between a bird and its environment is related to the dissipation of sensible heat and to its thermal insulation. Thus,

$$t_b - t_a = H \times (I + I_a), \qquad \ldots . (1)$$

where t_b is the body temperature of the bird,
t_a is the temperature of the environment,
H is the rate of dissipation of sensible heat,
I is the thermal insulation of the tissues and feathers,
and I_a is the barrier to heat dissipation provided by the air and surrounding objects.

If I is already at its maximum, and t_a then falls, clearly more heat must be made available by metabolism or t_b will fall. This rise of metabolism is partly due to activity and muscle tremors, and can be assisted by shivering. However, since birds often remain still in extreme cold, visible activity is not apparently necessary.

In hot climates the metabolism is no longer adjusted to requirements, but increases with rise of body temperature, so that homeothermy must then be maintained by evaporative cooling (page 316). It follows from this that there is an environmental temperature at which the metabolic rate is at a minimum, and this is called the critical temperature (*Figure 7.7*). The agricultural birds are large enough to have thick feathering, and the thickness can be regulated to give a wide range of insulation. So variation of metabolism, if reckoned as a percentage of basal, is less important to them in heat regulation than to small or heat adapted birds. Their critical temperature is also lower, and there is quite a large range of temperature over which the metabolic rate is nearly minimal; when it does rise the slope with falling environmental temperature is not very steep. For small and heat adapted birds the reverse of this is true. These characteristics of metabolism can all be deduced by setting up calculations on the basis of equation (1) above (Scholander *et al*, 1950b, 1950c). They are illustrated in *Figure 7.7*. If the metabolism per unit surface area were plotted in place of the metabolism as a percentage of basal, a similar picture would be obtained.

The rise in metabolism with falling temperature is not delayed until the bird has attained its maximum insulation by fluffing the feathers, etc. This is apparent from the curve for the cold adapted sparrow, whose critical temperature is 99°F., representing a climate in which the bird was undoubtedly under heat stress, in fact mild polypnoea occurred. In general the critical temperature of other birds seems to be close to the point where they have to increase heat dissipation by evaporation. The basal metabolism may, therefore, be just as correctly called the minimum to which metabolism can be reduced in response to warm climates, as the metabolism exhibited in a neutral environment, where no adjustment for temperature regulation is required.

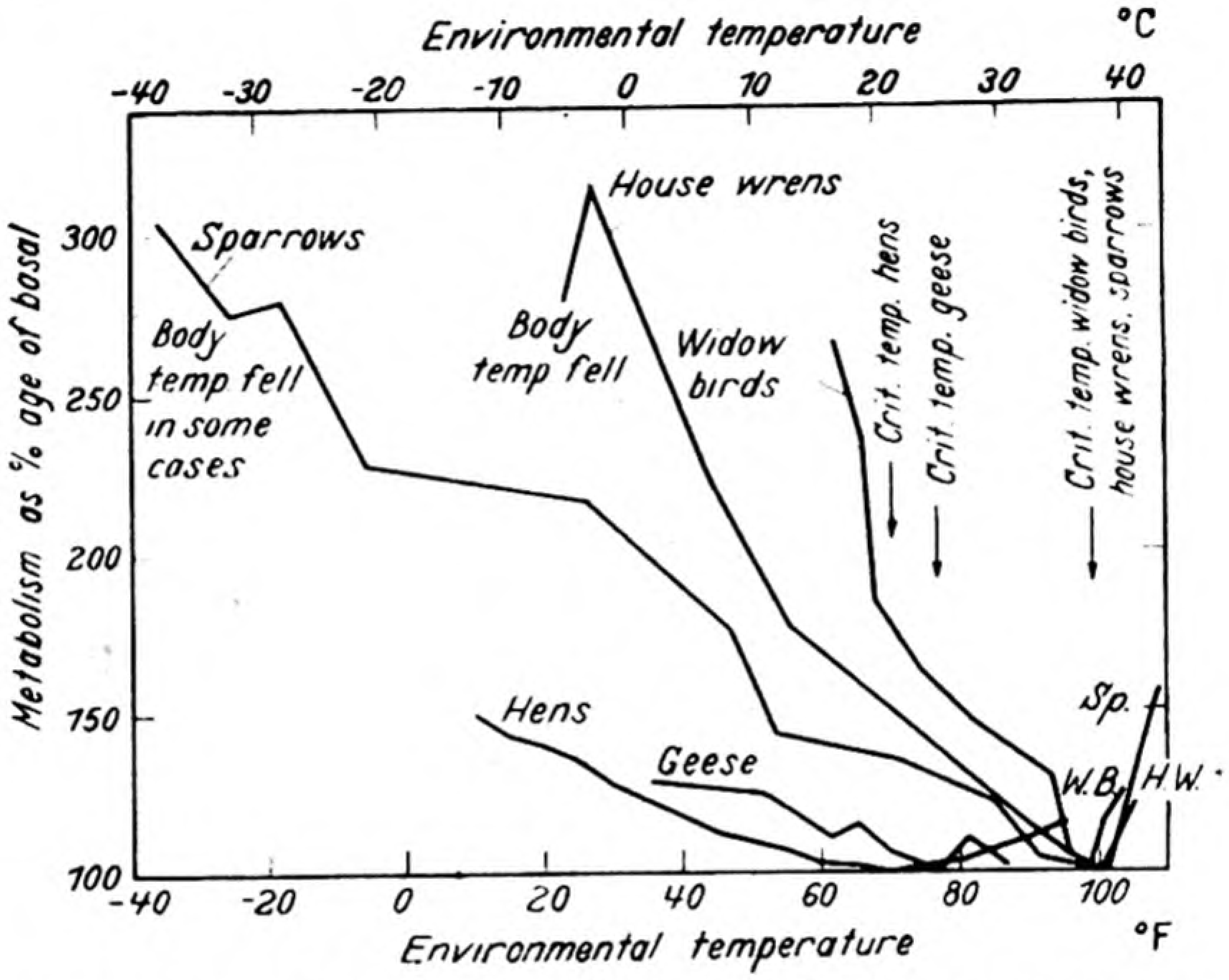

Figure 7.7. Effect of environmental temperature on fasting metabolism. The Widow bird (*Vidua paradisea*) and Eastern house wren (*Troglodytes aedon*) are very small birds, the former adapted to tropical, the latter to warm temperate climates. The house sparrows (*Passer domesticus*) used were cold-adapted (Widow birds after Terroine and Trautmann, 1927 ; Eastern house wrens after Kendeigh, 1939 ; house sparrows after Kendeigh, 1944 ; geese after Giaja, 1931, and Benedict and Lee, 1937 ; hens after Barott and Pringle, 1946).

If homeothermy is broken by extreme cold, the metabolism first rises to a maximum (summit metabolism), and then is reduced as body temperature drops further (*Figure 7.7*, house wren). In hypothermia it can fall much below the basal level.

Disease can influence the metabolic rate, and so interfere with thermo-regulation. For example, Herrick (1950) found that chickens infected with coccidiosis were less cold resistant than healthy birds. This was because they were unable to increase their metabolism in a cold environment to the same extent.

Nutrition.—Part of the energy of food is dissipated as heat (*see* Chapters 1, 2 and 3), so that the metabolism of an animal given food is greater than that of a fasting beast. It would, therefore, be expected that the critical temperature would be reduced on feeding. The effect, however, is not large in rats (BLACK and SWIFT, 1943; SWIFT, 1944). Benedict and Lee (1937) found that stuffed geese had a lower critical temperature than fasting birds, but did not estimate the size of the reduction. Owing to the effect of feeding on metabolism, the heat tolerance of fowls on a high plane of nutrition is less than that of birds subsisting on short commons (Robinson and Lee, 1947); the level of protein, within the limits of normal farming practice, has no effect. A high producing hen must eat more food to produce eggs, so this will tend to reduce heat tolerance. Her case, however, is not so critical as that of the dairy cow, who must dissipate the heat produced by a large population of micro-organisms in her rumen as well as her own heat, for these organisms multiply on a high plane of nutrition. In fact, HUTT (1938) in a field study of heat stroke found no evidence that fowls in lay were more susceptible than birds which were out of lay.

There is a diurnal rhythm of metabolism just as there is of body temperature (*Figure 7.8*), which is exhibited over a wide range of environmental temperatures (Kendeigh, 1944). It might be thought that in cool environments this characteristic would interfere with heat regulation. However, at night, when both the air temperature and metabolic rate are at their lowest, a diurnal bird does not need to be mobile. It can, therefore, fluff out its feathers to a greater extent, and adjust its posture to conserve heat.

Heat storage

On an average the heat content of the body of a homeotherm does not change, otherwise its temperature would not be constant. However, over short periods of time heat is gained or lost, especially when a temporary hyperthermia or hypothermia is induced. For large birds the mass and, therefore, heat capacity per unit area is greater than for small ones. So large birds have an advantage in an intolerable environment, just as large objects heat or cool more slowly than small ones in air of a different temperature.

Cardiovascular reactions

When a man is put in a hot climate a peripheral vasodilatation of the blood vessels in the skin and skeletal muscles takes place. This supplies the sweat glands with blood, and increases internal convection of heat from the centre to the skin surface. Birds have no sweat glands to supply; moreover, the feathers are a more important barrier to heat dissipation than the tissues. *Figures 7.9* and *7.10* illustrate this point. The temperature difference between the skin and the surface of the feathers is much greater than that between the rectum (centre) and the skin, except in hot climates, where much of the heat is dissipated by evaporation through the lungs. The effect of a peripheral vasodilatation would be to raise the skin temperature closer to the rectal temperature, increasing very slightly the temperature gradient through the feathers. The heat transfer through the feathers is proportional to this gradient, but the increase in it would be so small that little extra heat would be lost. Probably a vasoconstriction in cold climates would be equally ineffective, because few birds have much subcutaneous fat.

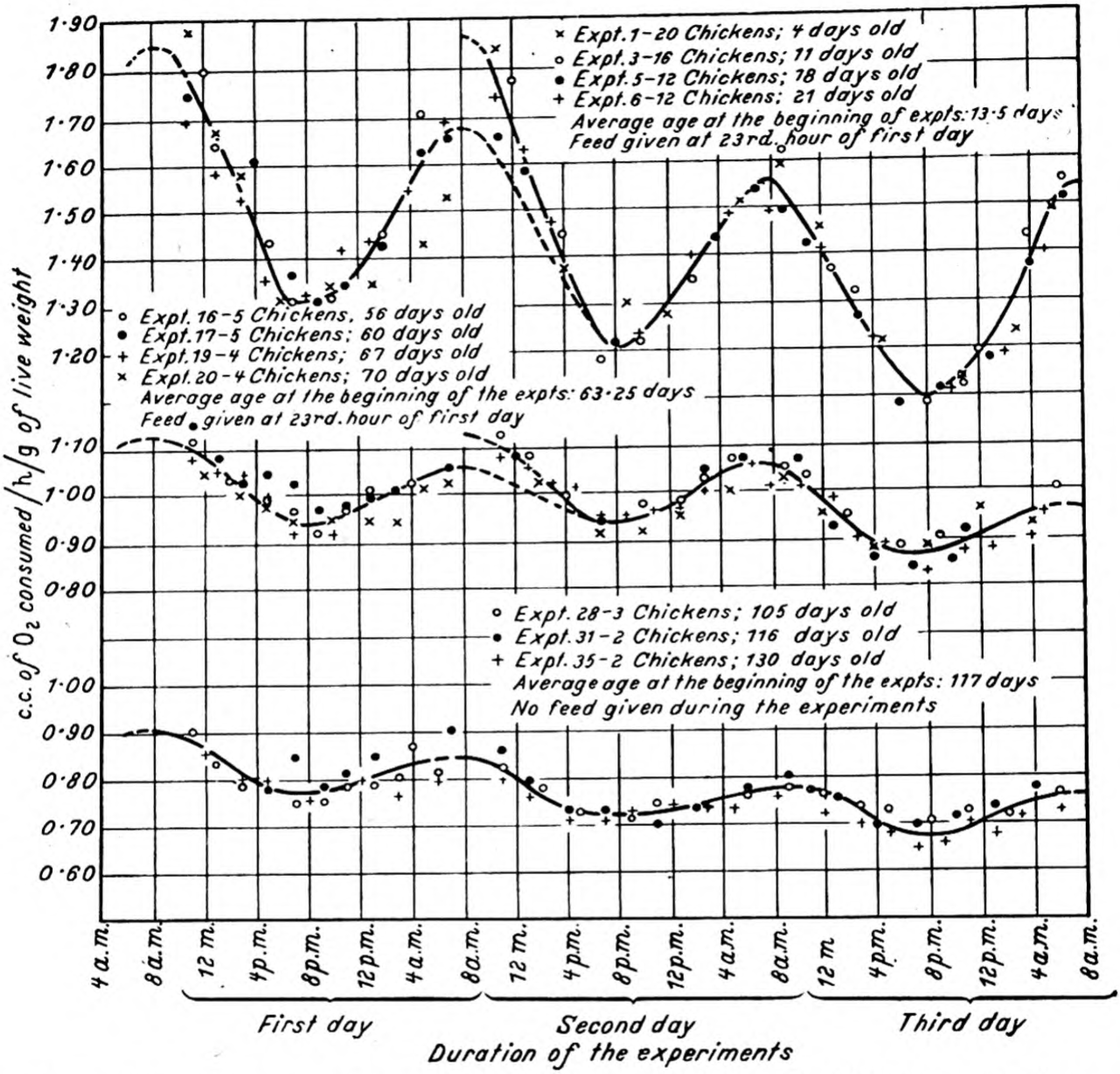

Figure 7.8. Diurnal rhythm of fasting metabolism of chickens. Ambient temperature 90°F.; humidity 22 mm. Hg vapour pressure; air movement slow. (From Barott *et al*, 1938, by courtesy *J. Nutrit.*)

In man longitudinal gradients along the limbs can be controlled by various means (Bazett, 1949) as well as gradients from the centre to the outside. In the cold the gradients to the extremities may be increased, so that the latter become cool and lose little heat. Thus, the brain and the inside of the body cavity gain insulation and conserve heat at the expense of the limbs, which may become uncomfortably cold.

Birds have extremities, which are poorly insulated, such as the comb, wattles, under surface of the wings and legs, so heat loss could be readily controlled by adjustment of their temperature. Scholander and his team (1950a) found that in ice-water the heat dissipation from the feet of arctic gulls was very small, corresponding to a circulation of only a few cubic centimetres of blood per hour, and, therefore, the establishment of a considerable longitudinal gradient. The gulls were able to walk around in snow at temperatures as low as – 58°F. without getting the feet frozen. To accomplish this they must either have been able to tolerate ice crystals in their feet, or to produce a vasodilatation in these very extreme conditions to prevent frost-bite. Although insect larvae in the Arctic can tolerate ice crystals, they cannot walk around when frozen hard, so it seems a vasodilatation occurred in the gulls. The same thing happens in a man's hand when it becomes unbearably cold (Bazett, 1949).

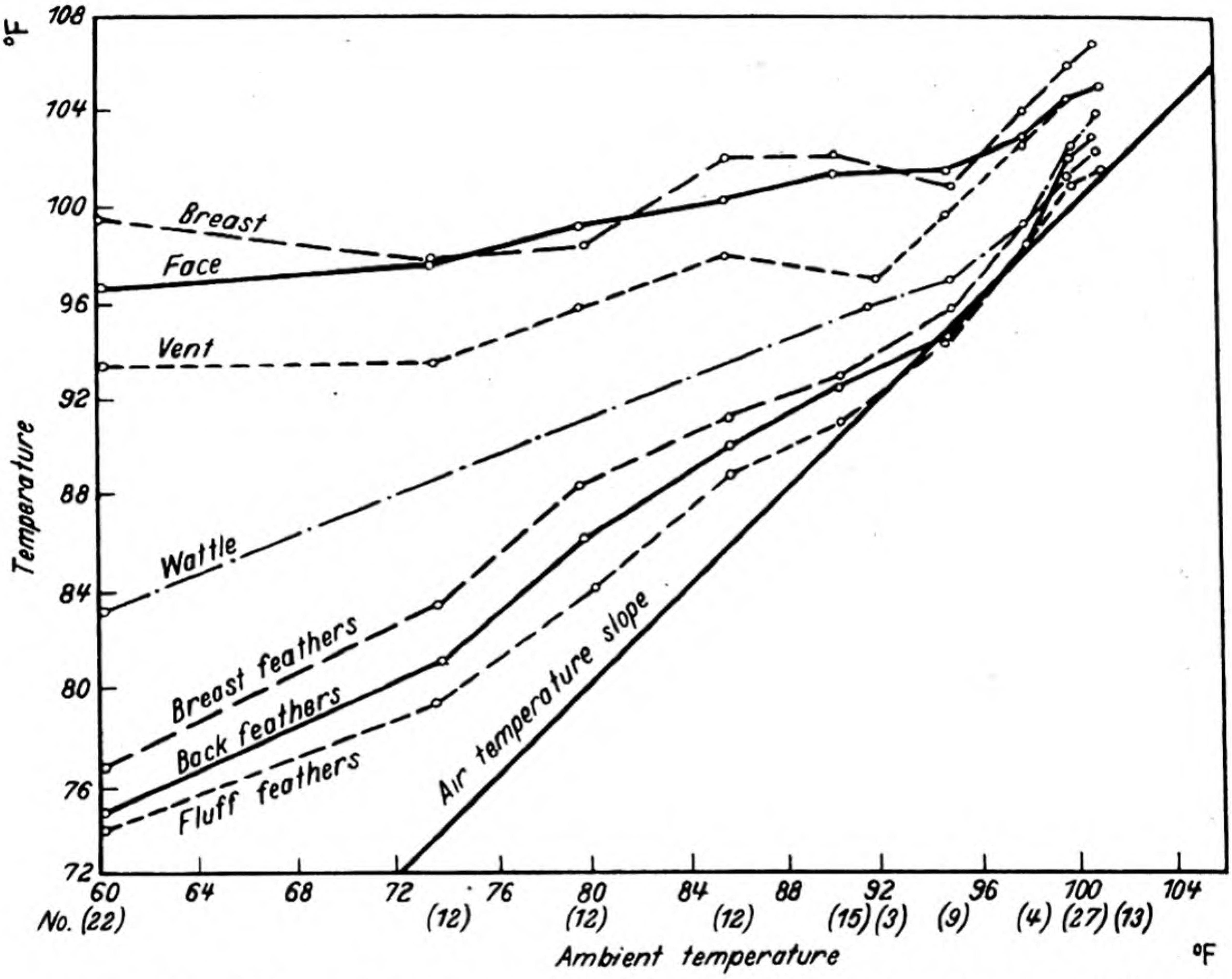

Figure 7.9. Skin and feather-surface temperatures of hens kept at different ambient temperatures, as measured with a dermal radiometer. Air movement 25 ft. per min. or less, radiation conditions not recorded. Figures in brackets are number of observations. Note the low feather-surface temperatures. (From Wilson, Hillerman and Edwards, 1952, by courtesy *Poultry Sci.*)

The comb and wattles, being uninsulated, must assist fowls to withstand heat, provided their temperature is above the ambient temperature. However, this has not yet been successfully demonstrated.

Heart rate.—The heart rate of man in thermal hyperpyrexia is increased. This is supposed to be due to the increased peripheral circulation, which as well as assisting dissipation of sensible heat, supplies the sweat glands with blood. High blood temperature may also exert a direct influence on the pacemaker. In fowls, as would be expected from the preceding discussion, the reactions are quite different. *Figure 7.11* shows the heart rate in thermal hyperpyrexia. Over most of the range of body temperature it is lower than in equable climates, not higher as in man (see also WILSON, 1948, 1949). At very high body temperatures, however, it rises to a high value. In these circumstances the fowls were agitated and restless in their cages, though quiet when picked up for observations. In the cold the heart rate rises in conformity with the increase in metabolism. If homeothermy is broken it falls with the metabolic rate.

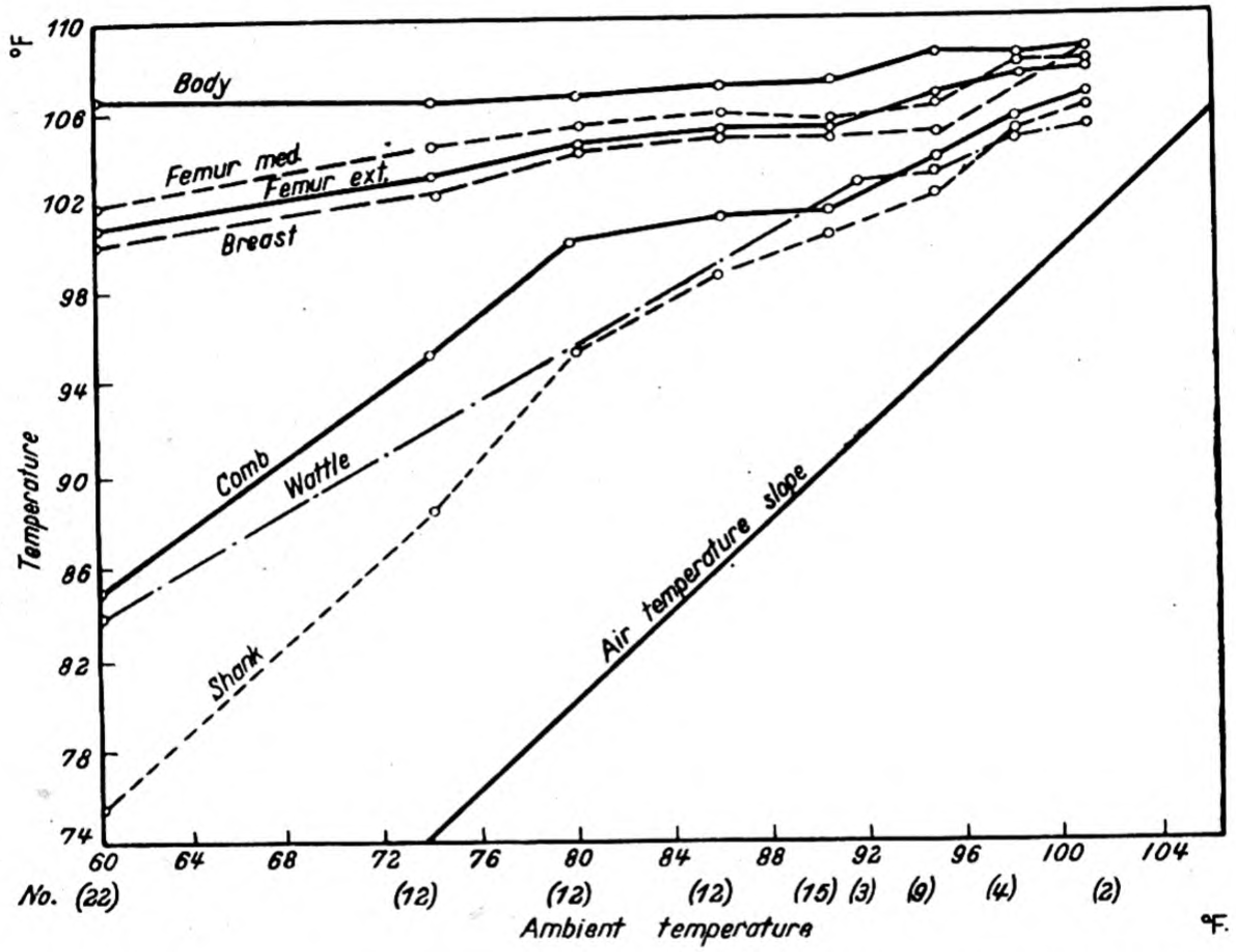

Figure 7.10. Skin temperature of hens kept at different ambient temperatures, as measured with a touch thermocouple. Body temperature means rectal temperature. Figures in brackets are number of observations. Note the high skin temperatures in comparison with the low feather-surface temperatures in *Figure 7.9*. (From Wilson, Hillerman and Edwards, 1952, by courtesy *Poult. Sci.*)

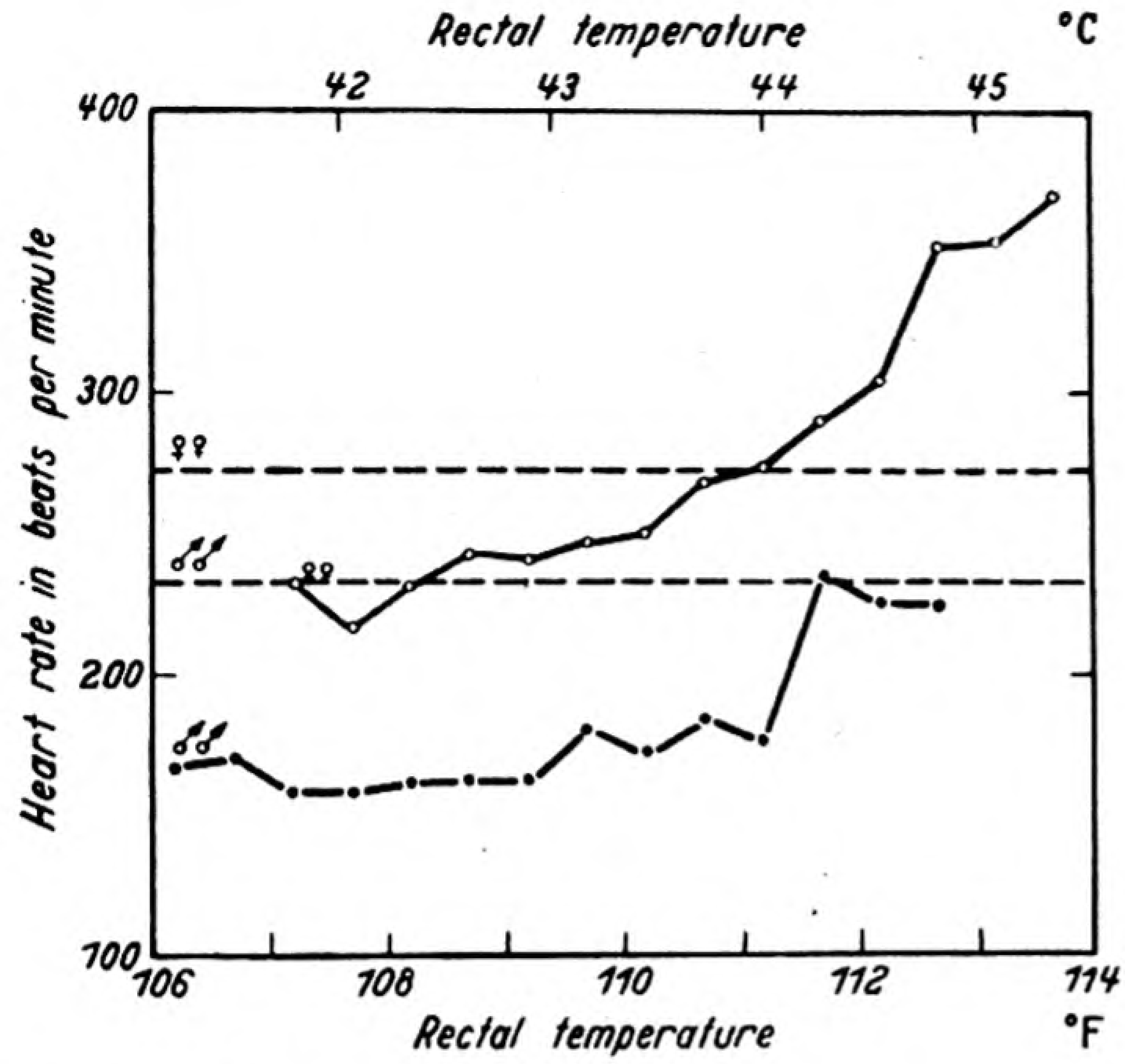

Figure 7.11. The relation of heart rate to rectal temperature of Brown Leghorn fowls in hot climates. Dry-bulb temperature 99–104°F. humidity 28 mm. Hg vapour pressure, air movement about 20 ft. per min. The broken lines indicate the heart rate of trained birds in an equable climate at normal body temperature. (From Hutchinson and Sykes (1953), by courtesy *J. Agric. Sci.*)

Evaporative cooling

The general principle of homeothermy is to maintain the body at a temperature above that of the atmosphere by a rapid heat production and a clothing barrier, both of which are adjustable. Most species, which live in hot climates, have surprisingly thick clothing, in many cases equivalent to a suit of battledress (Scholander *et al*, 1950a). Consequently, in a hot environment homeotherms must use evaporative cooling to dissipate their heat. When the temperature of the atmosphere exceeds skin temperature, evaporation must dissipate not only the heat produced, but also that which leaks in from the environment. Curiously enough the mode and efficiency of evaporation is quite variable between different species of mammals. It is almost as if evaporative cooling had been added to their system of thermoregulation as an afterthought, and were still evolving, for it reaches its greatest efficiency in man, a recently developed primate. Yet, it seems that evaporative cooling is in poikilotherms literally as old as the hills, for the cockroach, which has remained anatomically unchanged for 250 million years increases evaporation in the heat by a change in permeability of its cuticle (Ramsay, 1935). Similarly, the wet skin of amphibians tends to keep them at a more constant temperature than if they were dry, while some reptiles are reported to pant in the heat (Langlois, 1902, and later authors), though not so effectively as homeotherms.

Birds have no sweat glands, but accomplish evaporative cooling by panting; they do not salivate over their body like some mammals. A little water vapour diffuses through the skin. Panting starts in fowls in still air at an ambient temperature between 80–90°F. As hyperthermia develops in a hot environment the respiratory rate increases rapidly. Some Brown Leghorn hens, acclimatized to heat, can attain a rate of over 400 respirations/min., but the maximum for individuals varies (Hutchinson, unpublished observations).

The rate of evaporation of water from a plane surface depends upon the ventilation rate, and the difference in vapour pressure between the surface and the atmosphere. The vapour pressure at the surface is the saturated vapour pressure at the surface temperature. This should also be true for panting in birds. It must be emphasized that the vapour pressure of the air does not depend on its relative humidity, but on the absolute humidity, that is the amount of water vapour per unit volume. So a bird can evaporate moisture in a saturated atmosphere, whose temperature is below that of the respiratory passages. The temperature of these should be close to the rectal temperature, and in heat stress this is also true for the skin temperature over most of the body (*Figure 7.10*). Experiments in the author's laboratory show that the rectal temperature may, in fact, be taken as an approximation of that of the evaporative surfaces, so that at a given ventilation rate of the lungs the evaporative loss in a dry climate may be calculated from that in a humid environment or *vice versa*. The wetted area from which evaporation takes place is of course constant in birds, unlike sweating animals. Similarly, the air movement past the body has little influence, while in sweating animals it is important. A comparison of the effect of humidity on evaporation from birds and sweating animals is too complex to be made here, but some interesting information on the subject may be gleaned from a paper of NELSON *et al* (1947). Owing to the high temperature of evaporation humidity is less important in birds than in mammals which pant (see any psychrometric chart), and the amount evaporated per unit of lung ventilation is greater. Evaporation from sweating animals cools the skin, and, therefore, decreases heat loss by radiation and convection, though there is of course a net gain in heat dissipation (EICHNA and his associates, 1950). Panting in birds, on the other hand, brings into play a new cooling surface, the respiratory passages, without impairing heat loss by convection and radiation; in fact, it is increased by convection from the respiratory passages, provided the bird's temperature is above that of the atmosphere.

The heat absorbed from the body by evaporation may be taken as the latent heat at about the rectal temperature. It is true the vapour has to be cooled to atmospheric temperature, and expanded to the humidity of the atmosphere (HARDY, 1949), but these processes are likely to take place too far from the mouth of the bird to affect it.

Figure 7.12 shows the evaporative loss of Brown Leghorns in equable climates, and in various stages of hyperthermia up to the maximum which can be tolerated for 3 hr. The curve for 5 mm. vapour pressure represents about the driest, and that for 28 mm. the wettest hot climates that fowls are likely to meet in ordinary life. The rectal temperature, when below 108°F., depends on other factors besides climate, because the 'normal' body temperature is labile (page 300) so that the lung ventilation is not perfectly correlated with rectal temperature. This part of the curve is, therefore, not well defined, and depends partly on the circumstances of the experiment. The rise in temperature of the evaporative surfaces in hyperthermia increases the loss by an appreciable amount. The lower curves at each humidity show what the loss would be, if the temperature of the respiratory passages remained at 106°F. in hyperthermia. It represents, in fact, what the respiratory efforts of the bird accomplish. It may be seen that

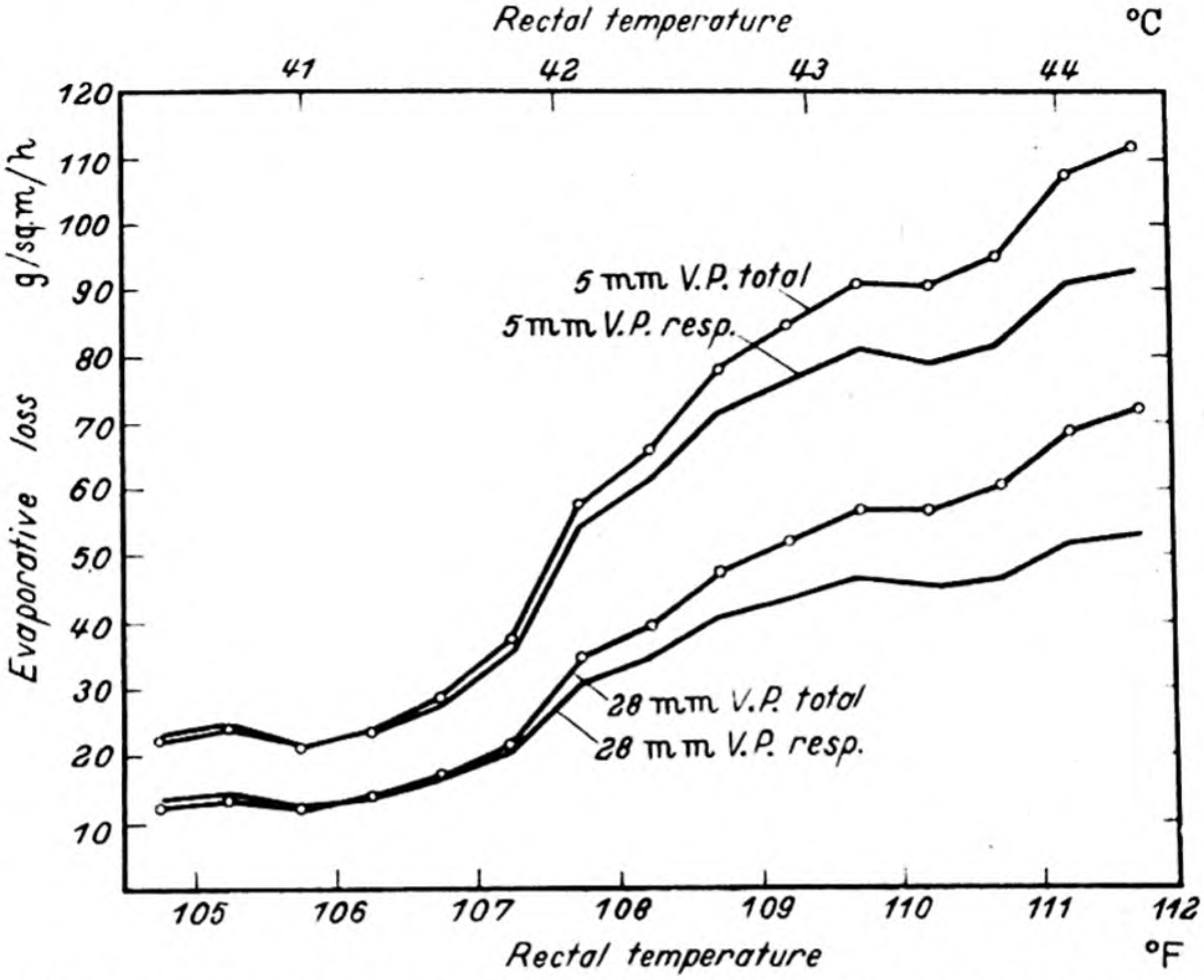

Figure 7.12. Evaporative loss of Brown Leghorns plotted against rectal temperature in equable and hot climates at two absolute humidities. It was estimated from insensible weight loss over periods of about 3 hrs. as described by Hutchinson and Sykes (1953). Most of the observations were made at 28 mm. Hg vapour pressure, but some were made in dry and intermediate climates. The raw data were corrected to 28 mm. or 5 mm. v.p. on the assumption, that evaporation is proportional to the difference in vapour pressure between the evaporative surfaces and the atmosphere, and that the mean temperature of these surfaces is the rectal temperature (see text). The lower curves at each humidity represent what the evaporative loss would be, if the temperature of evaporation were 106° F. at all rectal temperatures (see text). The surface area was calculated from the conventional formula, surface area in sq. cm = 10 × (body-weight in g.)$^{2/3}$. Range of body-weight, 1222–2300 g. (From unpublished data of Hutchinson.)

the lung ventilation increases rapidly between rectal temperatures of 107° and 109°F., but that after this there is little further increase. The increase in evaporation by respiratory efforts can be as much as 4 times. The fact that the respiratory rate can increase about 25 times suggests that the breathing in polypnoea is shallow, and von Saalfeld (1936) found that this was the case in anaesthetized doves, the depth of each respiration being about one-third of the normal. This shallow breathing and perhaps contraction of the parabronchial muscles (ZEUTHEN, 1942), hinders the pumping out of CO_2 and the risk of alkalosis.

At 28 mm. vapour pressure the maximum evaporative cooling of the Brown Leghorns was about equal to a unit of resting metabolism at the critical temperature, and about 1½–2 times at 5 mm. However, in extreme hyperthermia the metabolic rate may be at least double that at the critical temperature (ROMIJN, 1950). In consequence the fowls were not able to dissipate all their heat by evaporation; in fact, their rectal temperatures were always above the air temperature. In very hot countries such as India or northern Australia fowls are said to tolerate air temperatures over 110°F. If this is really so, birds resident in these countries must be able to dissipate all their heat by evaporation, unlike the author's Brown Leghorns. To do this either their metabolic rate must be lower, or their panting mechanism more effective. Another possibility is that in these hot localities the birds make use of micro-climates as described on page 326 *et seq.*

Kendeigh's house sparrows (1944), like the Brown Leghorns, could not dissipate all their heat by evaporation. Dogs have a great reputation amongst the mammals as thermal panting experts. Unfortunately there do not seem to be enough data to make an exact comparison of their performance with that of the fowl. However, it appears from SHELLEY and HEMINGWAY's experiments (1940) that they would be able to evaporate roughly 45 g./sq.m./hr. at 28 mm. vapour pressure with a hyperthermia of about 1°F. The Brown Leghorn does not attain this rate until a hyperthermia of 2·5°F. is induced. Man can easily produce enough sweat to dissipate the heat of 7 units of metabolism, and, if naked in a dry climate, is able to evaporate it, so his evaporative cooling is potentially far more effective than that of the fowl. Moreover, a very small rise in body temperature is necessary to initiate profuse sweating (LADELL, 1951).

Acclimatization

Acclimatization to heat or cold is a name given to the complex of processes which adapt an animal to the climate in which it has to live. The adaptation may be genetical by natural or artificial selection, or it may be physiological. In the latter case it may be the result of long or short-term exposure to particular environments.

Genetical acclimatization.—Nothing is known of the inheritance of cold or heat tolerance in birds. In the Philippines it was found that breeds of fowl originating in temperate climates did not do well (FRONDA, 1948). A local strain, the Los Banos Cantonese, the foundation stock of which were imported from a similar climate, were more successful. The adaptation of this stock to local conditions is not likely to be only a matter of heat tolerance, because breeds from temperate regions do reasonably well in hotter places than the Philippines.

There are geographical morphological variations within species of wild birds, which are supposed to be adaptations to climate. They can be only briefly listed here. For a detailed account reference should be made to MAYR's book (1942).

(a) *Bergmann's rule.* In warm-blooded species populations which live in a cool climate have a larger body size than those from warmer regions.

(b) *Allen's rule.* In warm-blooded species the relative size of exposed portions of the body (limbs, etc.) decreases with fall of mean temperature. On the other hand, the wings of birds are longer in cool climates.

(c) *Gloger's rule.* Melanins in feather pigmentation increase in warm and humid parts of the range. Reddish or yellowish-brown phaeomelanins prevail in arid regions where the blackish eumelanins are reduced.

(d) The stomach, intestine and caeca of birds that live on a mixed diet are relatively smaller in the tropical than in the temperate-zone races.

It should be emphasized that these are intra-specific not inter-specific rules. In any one environment birds of widely different size and conformation will usually be found living side by side. How far Bergmann's rule is really concerned with heat regulation is not very clear. For example, although large birds have some advantages over small ones in a cold climate, variations in size of the order of magnitude covered by Bergmann's rule would make very little difference. It might equally well reflect differences in availability of food during the rearing season, and it is known that populations of a species, which live in cool climates, lay more eggs, and so perhaps have enough food to rear more young than those in warmer places.

Long-term physiological acclimatization.—Nothing is known about this subject, whether, for example, rearing in a hot climate will give added heat tolerance in the succeeding pullet year. It is known that the thyroxin status of the dam can influence the thyroids of its chicks (McCARTNEY and SHAFFNER, 1949). Since the endocrine system is affected by acclimatization, it is by no means impossible that some effects of physiological acclimatization may be carried over from one generation to another without a change in genotype. LAMOREUX (1943) found that White Leghorn male chicks, reared from 32 days to 88 days at a temperature of 85°F., had combs three times the size of those of controls reared at 36°F. This should help them to tolerate hot climates in the following summer.

Short-term physiological acclimatization.—It has been known for a long time that the basal metabolism of small animals may be raised or lowered by exposure for a month or so to cold or hot environments. Thus, GELINEO (1934) found that the fasting metabolism of the greenfinch was affected not only at the critical temperature, but also at temperatures above and below it. HOFFMANN and SHAFFNER (1950) found that rearing chickens in a hot climate lowered the basal metabolism, and that this was correlated with changes in the thyroid gland, and in the rate of thyroxin secretion. Other endocrine glands also play a part in acclimatization, but there is very little definite knowledge on the subject. Although the increase in metabolism on acclimatization to cold should aid temperature regulation, it is doubtful if the summit metabolism is increased (ADOLPH, 1950).

WETMORE (1936) found that the number of feathers of Passeriformes was less in summer than in autumn after the moult. Moreover, some species put on nuptial plumage in the spring, and this is lighter than the winter plumage. Presumably these changes in plumage are mainly controlled by the day-length clock (*see* Chapter 8), or caused by attrition, and are not a direct response to the temperature of the environment. They should, therefore, be distinguished from the growth of hair of HOESSLIN's dog (1888) or HAGENBECK's giraffes (1911), which was a direct response to cold. However, Hagenbeck also states that ostriches, kept out of doors in temperatures as low as 7°F., grew extra thick plumage, so it is possible there can be a response to cold in some birds. Laying hens cannot grow feathers to any appreciable extent, so any adjustment of plumage in their case must be conditioned by the climate before, not after the annual moult. The feathers of cocks, on the other hand, continue growing for a number of months after the onset of moult (Greenwood, 1936).

Effect of short-term acclimatization on heat tolerance.—It is well known that short daily exposures to severe heat stress can increase the working performance of man in a hot environment, and that the maximum adaptation is gained after about 14 days. This short, sharp treatment is more effective in improving physical performance than continuous residence in milder conditions. The fowl likewise can learn to tolerate heat better after a series of short sharp exposures, and continuous residence in milder climates is also effective (HUTCHINSON and SYKES, 1953). After 24 successive daily exposures of up to 4 hr. to a dry-bulb temperature of 99°F. at a high humidity and low air movement, a dry-bulb temperature of 102·5°F. would give about the same hyperthermia as that produced in the first few tests (*Figure 7.13*). Residence after this in a milder climate for 3–4 weeks further improved heat tolerance, but only after a few additional short exposures to extreme climates. The final performance showed an improvement of about 5°F. in terms of environmental temperature. This is not very large, but it was found to be as important as the constitutional variations in heat tolerance between hens of the same breed. If the tests of heat tolerance were conducted at night, the improvement was less, suggesting that quieter behaviour contributed to the enhanced performance after acclimatization, for there was of course more room for such behavioural change in the day-time than at night.

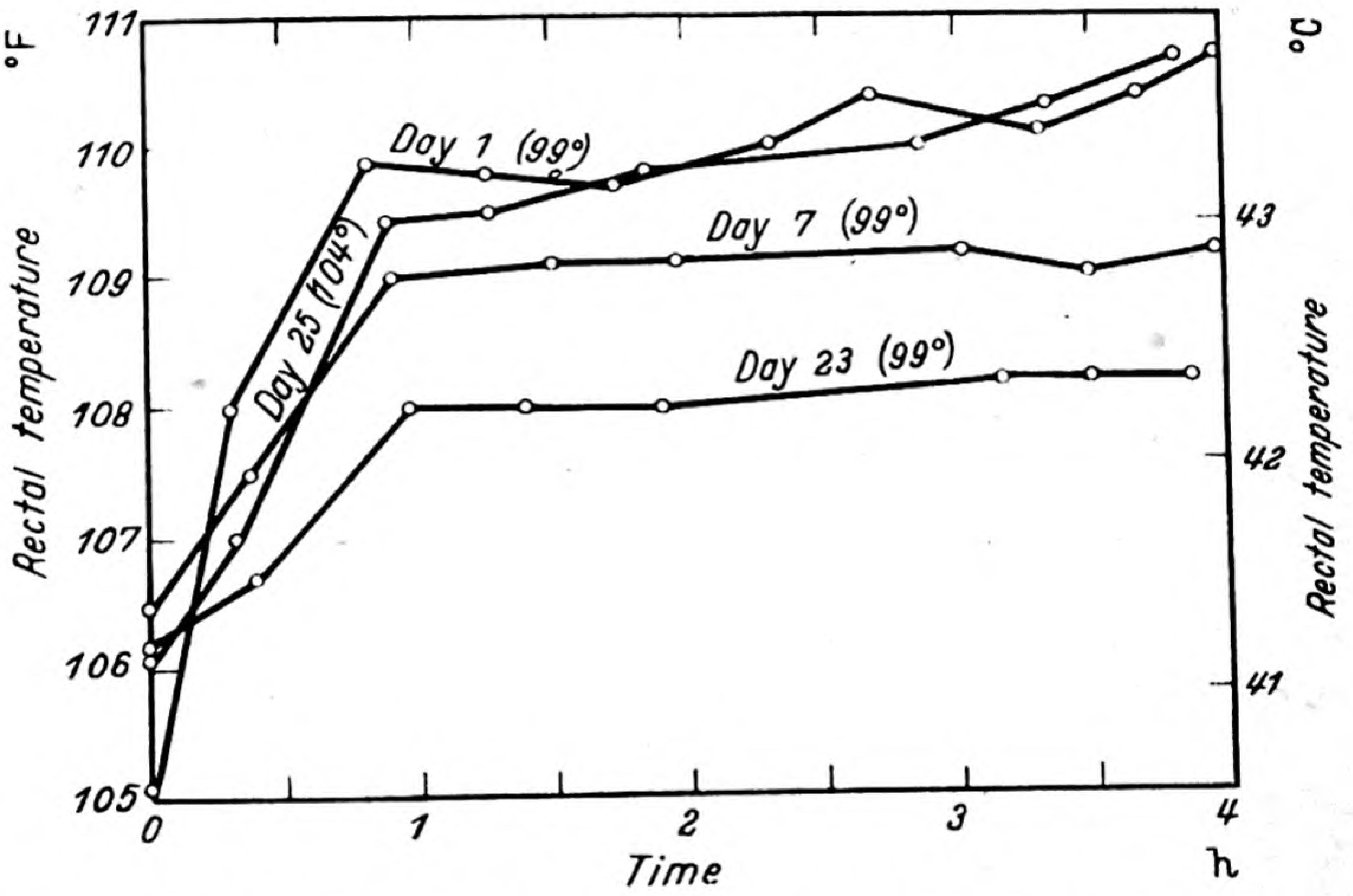

Figure 7.13. Acclimatization to heat by short sharp exposures. Rectal temperature of a cock during 4-hr. daily exposures to a hot humid climate at various stages of acclimatization. Day 1 means during the first daily exposure, day 7 during the 7th exposure and so on. Figures in brackets on the curves indicate the dry-bulb temperature of the environment in °F. The mean radiant temperature was 0·6°F. below the air temperature. The humidity was 28 mm. Hg vapour pressure, and the air movement about 20 ft./min. in all tests. It may be seen that on the 25th day the rectal temperature at 104°F. air temperature was close to what it was at 99°F. on the first day. The improvement of this bird was rather greater than the average (see text). (From Hutchinson and Sykes, (1953), by courtesy *J. agric. Sci.*)

In man increased sweating plays a major part in the acclimatization observed. In fowls by contrast no increase in evaporative cooling was found during severe heat stress; in fact, in a given hot climate evaporation was less in acclimatized than in unacclimatized birds, because the hyperthermia was less. There was, however, some evidence that the polypnoea was more rapid and shallower after acclimatization. This might reduce the tendency to alkalosis from pumping out CO_2, and perhaps also the work of respiration.

The fact that heat tolerance is labile, in the sense that it depends upon acclimatization, means that reactions to heat stress, such as increases in rectal temperature, respiratory rate and evaporative loss, cannot be satisfactorily expressed in terms of climate, unless the degree of acclimatization is specified. Similarly, acclimatization must be taken into account, when the heat tolerance of fowls resident in different localities is compared. Neglect of such precautions, and the effect of varying economic status have made interpretation of similar racial studies on man difficult.

ECTOTHERMIC CONTROL

It was mentioned at the beginning of this chapter, that animals can regulate their body temperature by suitable behaviour, as well as by internal physiological mechanisms. Poikilotherms, which have little endothermic regulation, are naturally greatly dependent on ectothermic methods. For example, SERGEYEV (1939) describes how a lizard and a tortoise contrived by sitting in a burrow, or moving into the sunshine, or under or into a bush to maintain a fairly constant body temperature. Similarly, BOGERT (1949) found that the average day-time body temperature of species of different genera of diurnal lizards was well defined and characteristic of the genera, although observations were made in two distinct field climates. Naturally the temperature of individual animals varied, because poikilotherms, unlike homeotherms, are adapted to carry out their normal activities over a wide range of body temperature. Of the mammals man is the greatest ectothermic expert. He owes his skill to the combination of a well developed brain, and a complex social organization. His naked skin and powerful sweating mechanism, though admirable for ' mad dogs and Englishmen ', are quite unsuited to a sedentary life in a cool environment. Therefore, in his case ectothermic contrivances are a necessity. Adult birds like other kinds of animals make use of ectothermic control.

Posture and activity

On exposure to heat, fowls become exceedingly sluggish, so reducing the metabolic heat load as far as possible. If the climate is a mild one, they may go to sleep even in the middle of the day. If the climate is too severe for the birds to tolerate, they become restless at a rectal temperature around 111°F., and may become very agitated at 112°F. This agitated behaviour works against homeothermy, causing a vicious circle, which has also been observed in cases of heat stroke in man. A fowl, standing in a hot climate, holds its wings slightly separated from its body, so that air may circulate past the poorly insulated undersurface (*Figure 7.14*). If the bird lies down, which it does much of the time, it usually adopts a rather extended position (*Figure 7.15*). Sometimes the head and neck are stretched forward, and the head often lies on the floor of the cage.

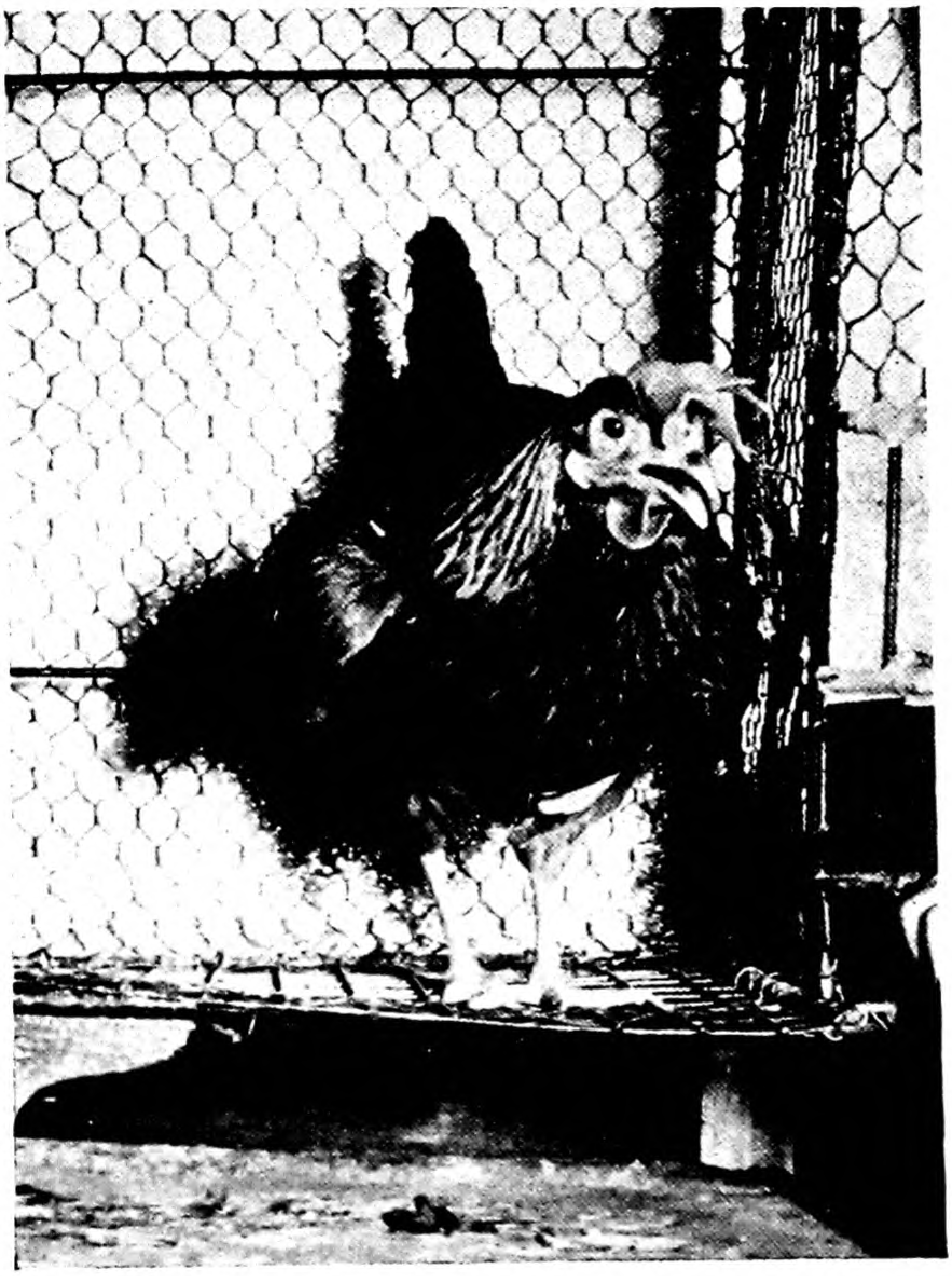

Figure 7.14. Brown Leghorn hen standing in a hot climate. Note the wings held out from the body, so that air circulates underneath.

Most fowls, like cattle, will drink large quantities of water on exposure to heat, throwing a good deal over their combs and wattles (Robinson and Lee, 1946; Wilson, 1948). This excessive drinking seems to be increased with acclimatization. Turkeys in the heat behave much like fowls. Ducks on first exposure, sit quietly with heads tucked under their wings. Later, when they begin to feel the effects of heat, they splash large quantities of water over their feathers, ruffling them with their beaks, and rub the oil glands continually (Robinson and Lee, 1946).

In cold weather a fowl, when standing still, tends to be rather hunched up, thus reducing the surface area (*Figure 7.16*). The feathers, especially over the breast, are fluffed out. If the bird becomes active, the feathers lie down again, but are fluffed out as soon as the bird stops. In cool conditions birds are usually active, but in very extreme cold they spend a good deal of their time inactive and fluffed out, as if the increase in insulation was worth more than the increase of metabolism during activity with its coincident heat loss by ‘ bellows action ’, and reduced fluffing. At night, when the metabolism is at its lowest, a bird even in quite a mild climate is thoroughly fluffed out (*Figure 7.17*), and sleeps much of the time with its head under its wing. Putting the head under the wing reduces heat dissipation by about 12 per cent (Deighton and Hutchinson, 1940).

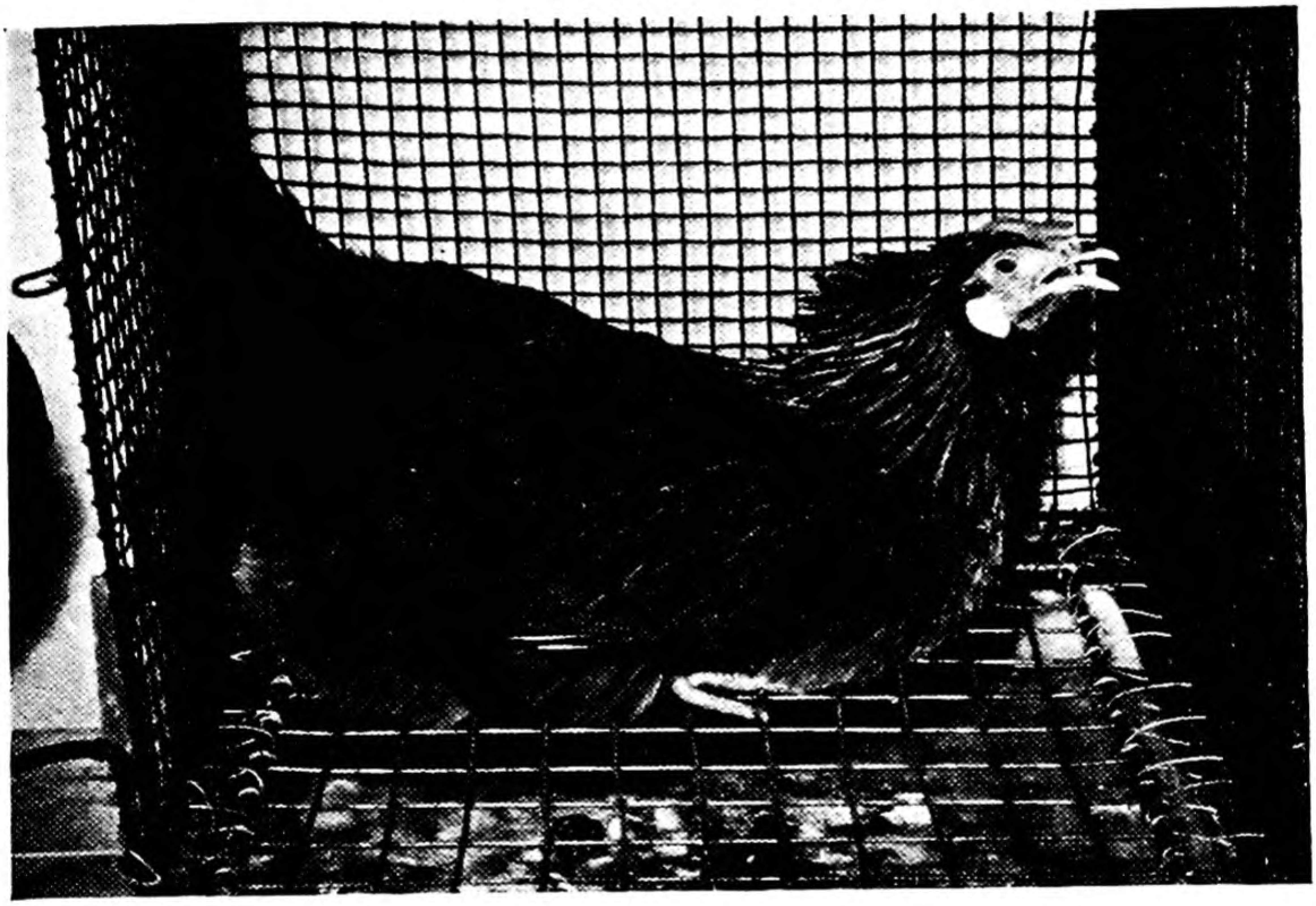

Figure 7.15. Hen lying down in a hot climate. Note the leg partly extended.

Migration

Birds, because they can fly, are able to travel enormous distances from unsuitable to favourable environments. In this way they can avoid seasonal changes of climate, but it may be that migration is more important for ensuring the food supply, particularly in insect-eating birds, than in maintaining homeothermy; for many species of all sizes can tolerate considerable extremes of climate. The fowl and turkey are non-migratory, but ducks and geese in their wild state migrate. In fact, the art of eider-farming is to persuade the eiderduck to end its travels on the farmer’s beach. To achieve this he makes sheltered nesting boxes (ectothermy), and decorates them in such a way as to please the ducks.

Micro-climates

Adult birds seem to have less need of micro-climates than the smaller mammals. For example, they can live in the open in daytime in arctic climates, which compel small mammals to spend most of their time in underground nests (Scholander *et al*, 1950a). Many avian species do, however, roost in holes, and most prefer sheltered places.

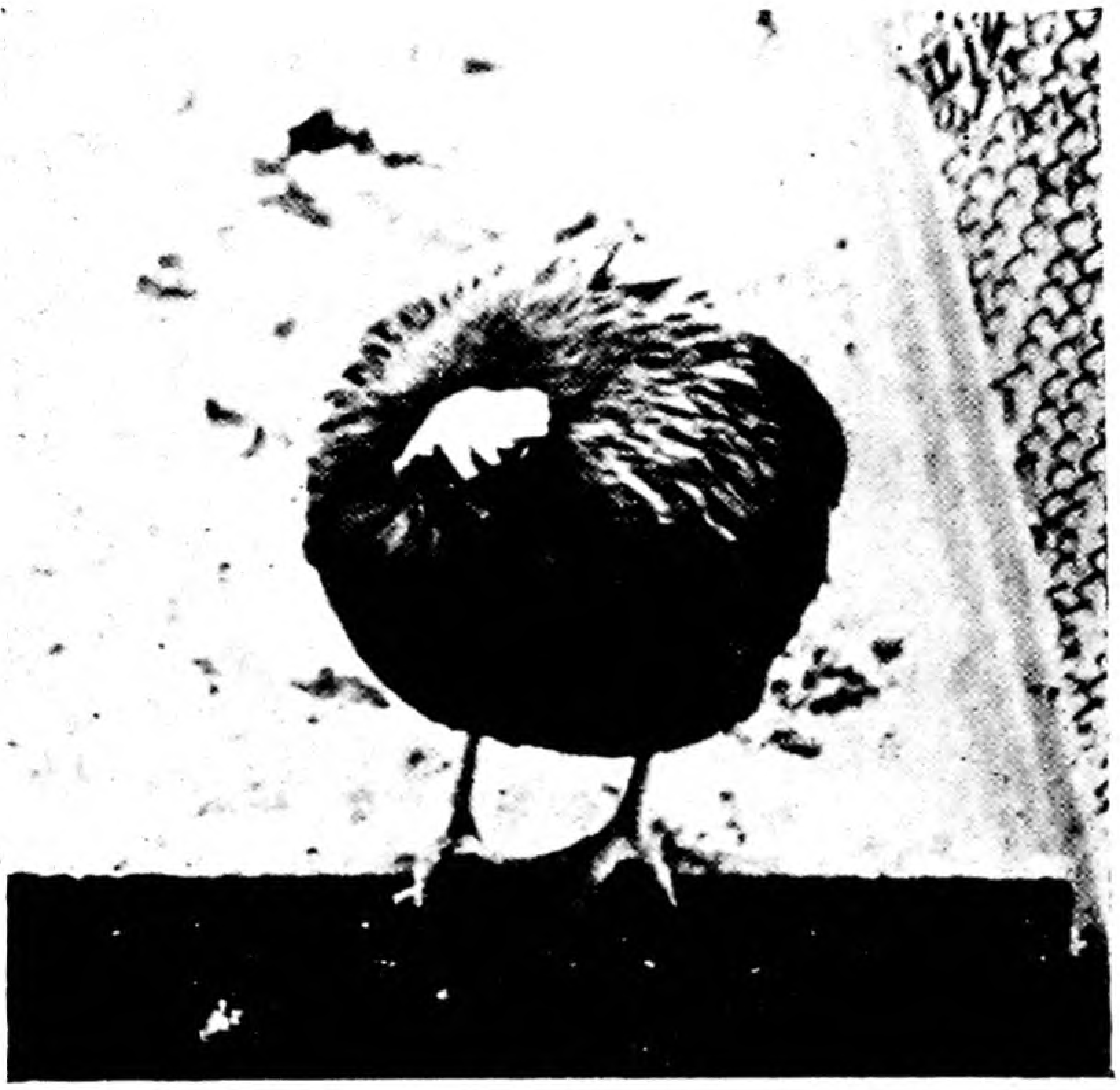

Figure 7.16. Inactive Brown Leghorn hen fluffed out on a cold morning.

Agricultural birds will make some use of micro-climates, if given a chance. For example, on hot days fowls will seek cool and shady spots, while ducks cool themselves in water. The provision of shade and cool housing is therefore important in hot climates. In the tropics fowls are often kept on range under coconut groves, where they can continue to feed during the heat of the day. The ground, if damp, is a good heat conductor, and is cool in the shade. So if a bird is sitting in an atmosphere hotter than its body, heat passes right through it from the dorsal to the ventral surface, just as it does through an Australian bushman, when he sleeps naked beside an open fire on a frosty night (WULSIN, 1949). This can also happen in strong solar radiation at a lower air temperature. Under these circumstances the thick insulation of the dorsal feathers and the still air just above them impede the flow of heat into the bird, while the squashing of the breast feathers facilitates its passage out to the cool earth (*Figure 7.18*). In this micro-climate ordinary meteorological observations of temperature, air movement, humidity and radiation give little indication of the real heat stress on the bird. In hot weather the hen instinctively dusts in litter or soil that is cooler than her body (WILSON *et al*, 1952). CARD (1952) notes that concrete floors, which are slow to warm up in hot weather, aid heat dissipation.

Association with man (including poultry housing)

The fowl, because it is useful to man, has become incorporated in his cultural system. In this association it can make use of man's efficient ectothermic contrivances, for his complex social organization enables the production of suitable housing equipment. Over the last few years the large price differential between summer and winter eggs in the United Kingdom has caused more attention to be paid to housing. In fact, the industry is now seriously considering the advisability of artificial heating, which as well as increasing production might save a little food (*Figure 7.7*). In Scandinavia the body heat of pigs is used to keep the sties warm. Fowls similarly will provide some heat, which can be conserved if the housing is good enough; 500 hens produce per day the same amount of heat as the combustion of 40 lb. of coal (Card, 1952).

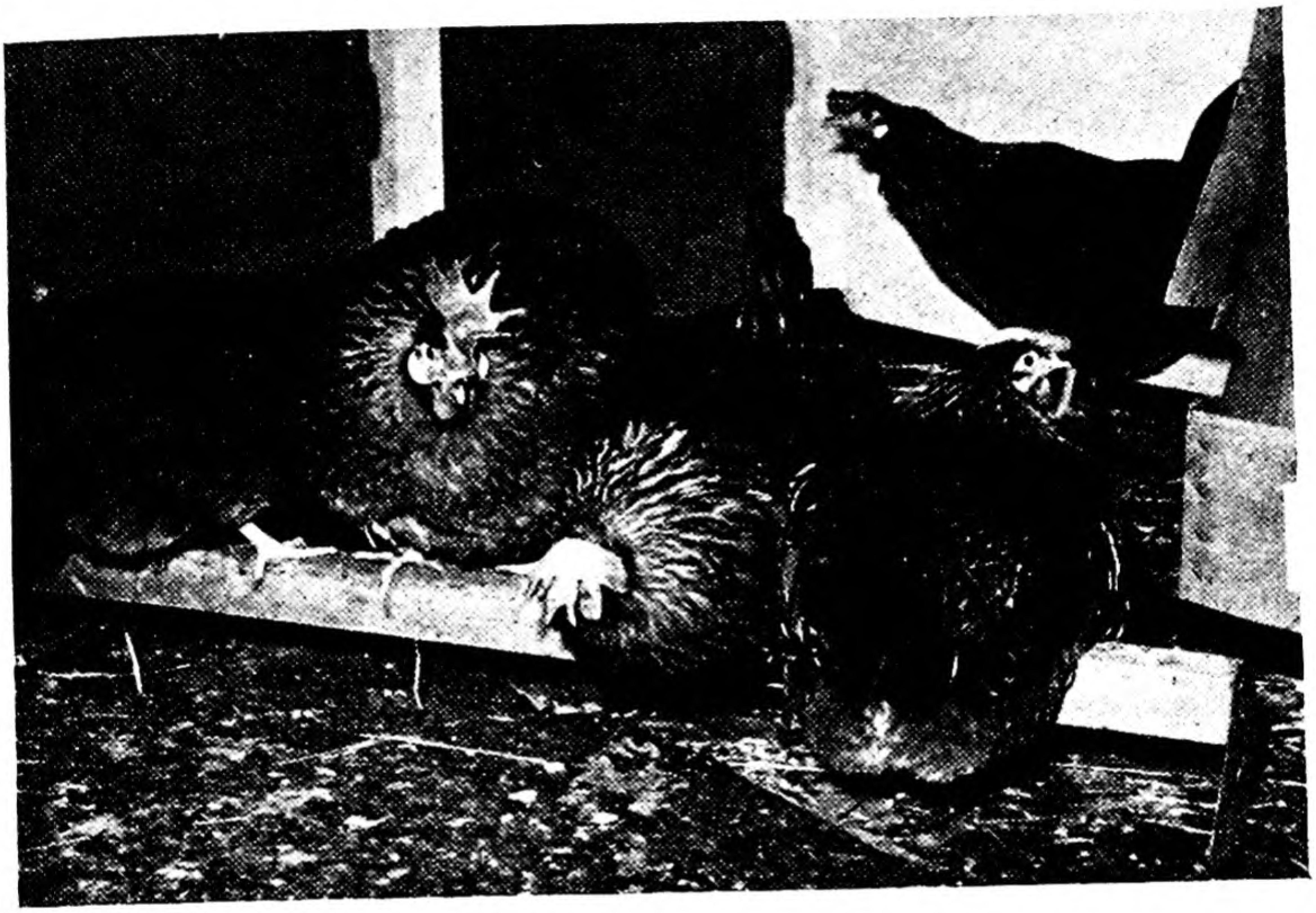

Figure 7.17. Brown Leghorn hens retiring to roost at an ambient temperature of 23°F. in one of the climatic chambers at the Poultry Research Centre, Edinburgh. The hen in the background is still active, and does not need to fluff completely in this climate. Those on the perch are either already fluffed out or in process of fluffing.

A detailed account of poultry housing will be found in Card's book. In this chapter general principles only will be outlined. Heat insulation of the roof is important in both hot and cold conditions. On cold nights it impedes radiation of heat to the sky. On hot days it prevents conduction of the heat of solar radiation into the house. In a cold environment insulation of the walls hinders the conduction of heat produced inside the house to the surrounding atmosphere, or in hot weather the passage of heat inwards from outside. Insulation of the floor as well as preventing heat loss also keeps it dry. An uninsulated floor tends to follow the temperature of the ground rather than that of the air. When the ground is colder than the atmosphere, the temperature of the air in contact with an uninsulated floor may be below the dew point, so that condensation takes place. Even if the floor temperature is just above the dew point, the relative humidity in this micro-situation may be high enough to impede evaporation of the excreta. Similar trouble may arise in variable weather with concrete floors, the temperature of which lags behind that of the air. Consequently, it is not surprising that the use of the deep litter system has spread so rapidly; for its insulating value and heat of fermentation keep the floor dry, and warm the building without costing the farmer anything in fuel. It was used in the early years of the century by Hagenbeck (1911) to heat his acclimatization-house for large mammals. The drive for winter eggs has caused its recent application to poultry.

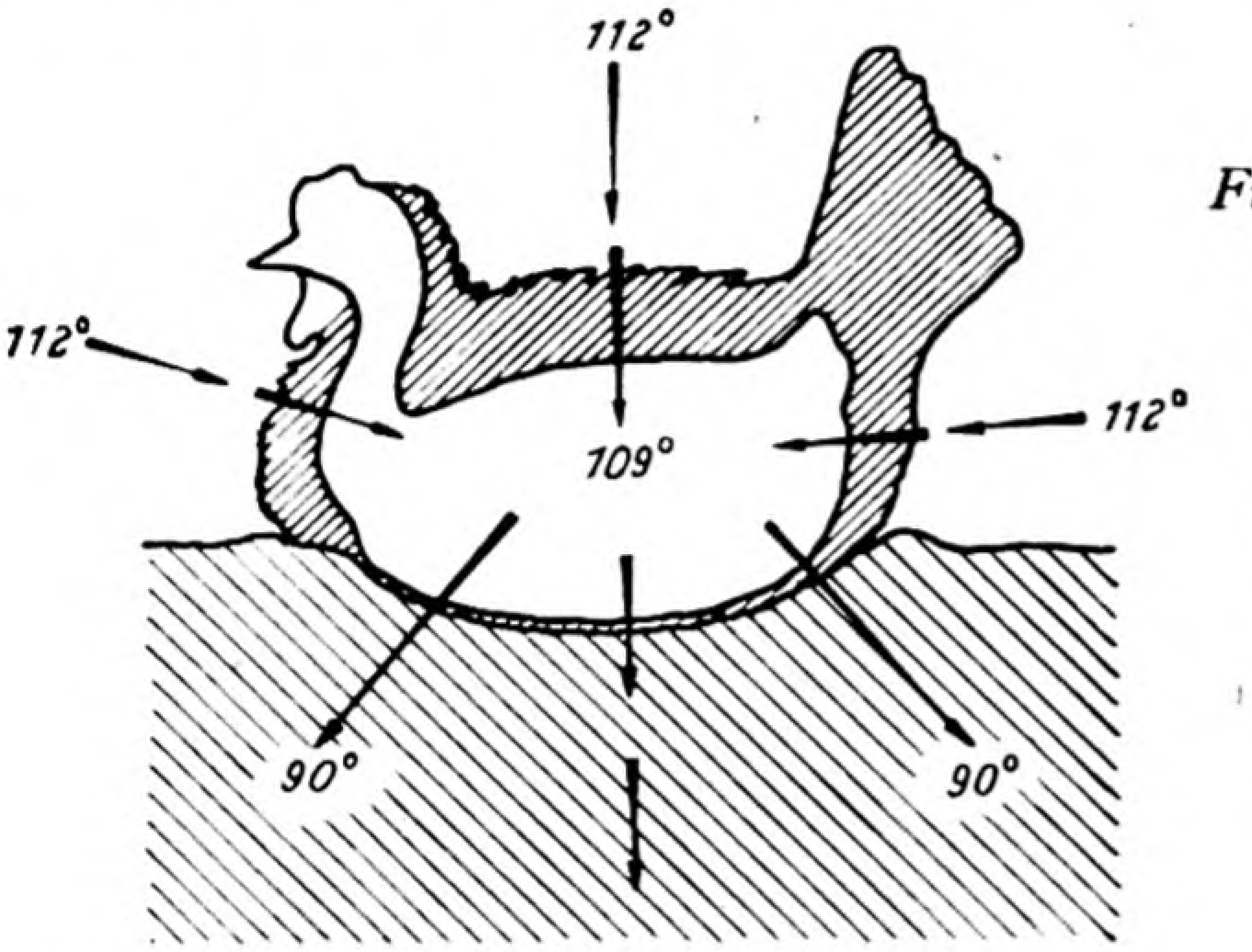

Figure 7.18. Heat transfer through a fowl to cool ground in an extremely hot climate. The hatched area represents the feathering. The arrows show the heat flow and the figures indicate temperature in °F. Note that the feathers impede the flow of heat from the air into the bird more than the flow from the bird to the ground.

Ventilation is an important consideration in designing poultry houses. In cold weather it should be reduced enough to prevent excessive loss of heat, but not so much that the air becomes foul, or the house damp. The inlet ventilators should be so designed that local cold draughts are avoided, for although there is little scientific information on the subject, most animals, like man, abhor such draughts. In a hot environment natural cross-ventilation from windows on either side of the house is effective, preventing the temperature rising much above that of the outside air. In addition, the general air movement inside is increased, which, provided that the air is below the skin temperature of the birds, may help to keep them cool.

In extreme conditions it may be necessary to cool hens with water. For this purpose mist spraying is most effective. Spraying a hen for 30 sec. with only 40 ml. of water will keep it comfortable for 60–90 min. (WILSON and HILLERMAN, 1952). In fact, it may be said that heat stroke under intensive conditions is the result of bad husbandry, not an intolerable climate. Immersion of the whole bird in water, except in emergency, is unwise, for the hyperthermia is in these circumstances often succeeded by a hypothermia (Wilson and Hillerman, 1952; Hutchinson, unpublished observations). This is because the feathers take some time to dry out, and because the thermoregulatory system may be for a time deranged.

It was mentioned earlier that the evaporative cooling of fowls is not greatly affected by a change of humidity, and this will be further discussed later in the chapter (pages 347–348). It follows from this that, if the temperature of a poultry house is reduced by evaporation of water, the heat stress on the fowls will tend to be alleviated, even though the humidity is raised. Water blinds, which cool the inlet air by evaporation, are found to be effective. Mist-sprays, as well as cooling the hen directly, also reduce the temperature of the air. These devices are of course more effective in dry than in wet conditions, but this does not matter much since high maximum temperatures are far more common in dry climates. If evaporative cooling is applied by spraying the roof, the humidity is, of course, not raised inside. However, this method is less effective than internal evaporation, except where the roof is poorly insulated. Another method of reducing the temperature in a house, which has deficient roof insulation, is simply to whitewash the roof. This reduces absorption of solar radiation.

Human assistance in the heat regulation of the fowl does not only increase the yield of eggs at certain seasons of the year, it can also lead to changes in the general system of husbandry. Thus, TEMPERTON (1952) finds that, if the birds are warmly housed and artificial lights are used, part of the stock may profitably be hatched in November and December. They come into lay in April or May. In the autumn not more than 10 per cent moult, so that high winter production with large eggs is secured. The birds are sold off in February and March. This system spreads out the rearing season, and enables the carcasses to be sold at a time when they will fetch good prices, yet a full season of production is achieved.

HEAT REGULATION IN YOUNG BIRDS

ENDOTHERMIC CONTROL

Embryos of birds have no endothermic means of temperature regulation. If they had, it would be of little use to them, for during most of the incubation period the surface area of the egg is large in comparison with the size of the embryo, and there is no heat insulating cover. Consequently, the temperature of the embryo is always close to that of the surrounding air. However, as it develops, its metabolism increases, and in the later stages of incubation the temperature is slightly above the air temperature (*Figure 7.19*), so that there is some heat dissipation by convection and radiation. In this respect the embryos are different from poikilotherms, in which the heat production is normally balanced by evaporation.

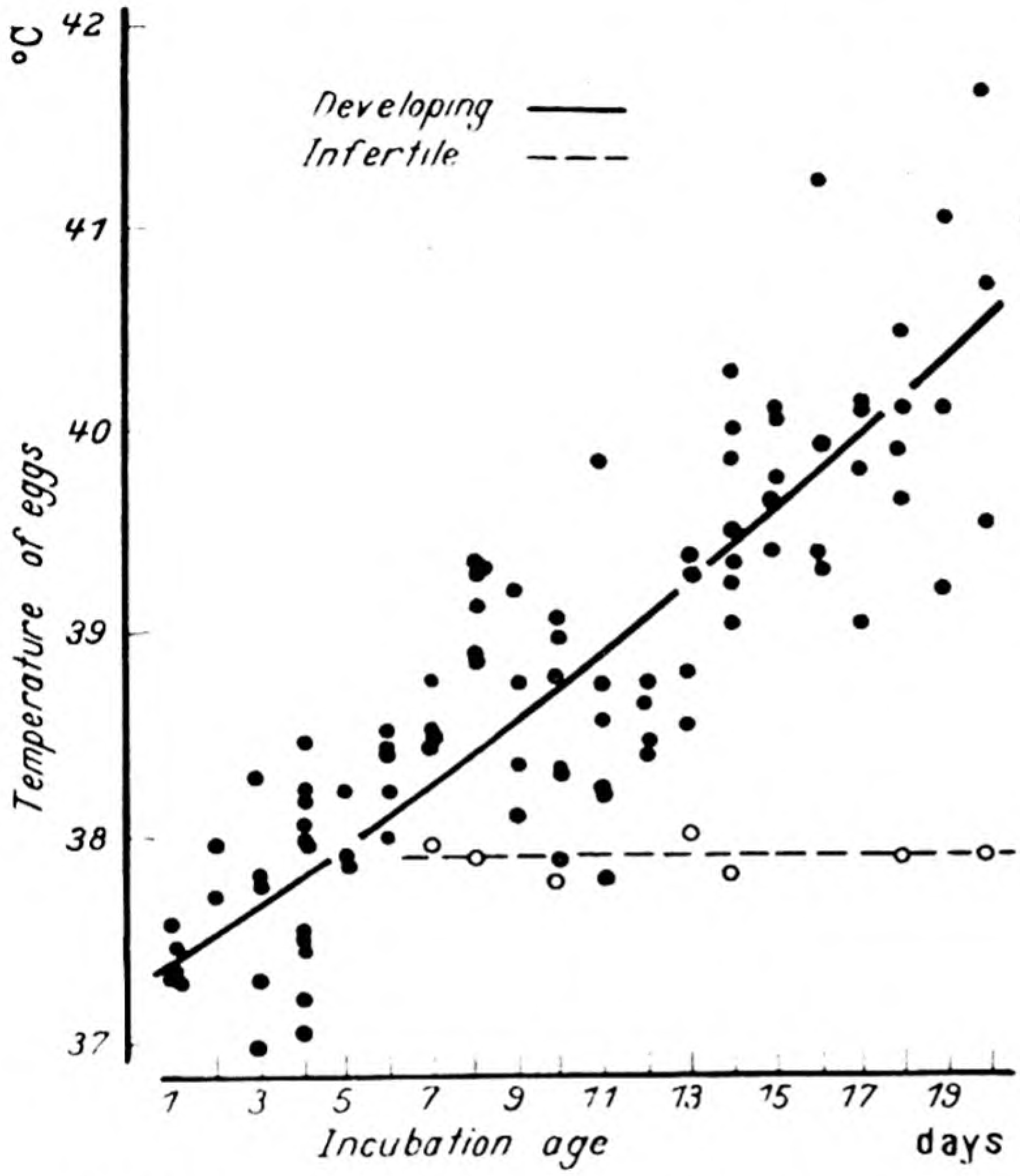

Figure 7.19. Temperature changes of developing hen's eggs. Each dot represents the average value of several measurements on an individual egg. Circles indicate the temperature of infertile eggs. The observations were made in a glass-topped incubator at a temperature of 37·75°C. (99·95°F.) at the level of the thermocouple used. (From Romanoff, 1941, by courtesy *Science*.)

Chicks are divided into two classes, precocial and altricial (Edwards, 1824). Birds of the precocial class to which all agricultural birds belong, are provided with down on hatching. As soon as this dries out the body temperature rises further above the air temperature. In addition, at about the time of hatching the chicks develop the power of increasing their metabolic rate during cold stress like other homeotherms (Pembrey, Gordon and Warren, 1894–95). They can also increase evaporative loss in heat stress by panting. They are, in fact, essentially homeotherms adapted to a hot climate, but because they are heat adapted, the range of climate over which they can regulate body temperature is necessarily small (Scholander *et al*, 1950b, c). However, when provided with waistcoats, chicks can regulate their body temperature well enough, and with this ectothermic aid they are reared without artificial heat by peasants in Egypt, a country which has a large diurnal rhythm of environmental temperature. As the chick gets older, it becomes adapted to lower temperatures. This is accomplished by the growth of feathers and an increase in the basal metabolic rate per unit surface area. *Figure 7.20* shows this increase in metabolism, which is later reduced, when the adult plumage is developed (*see also* MITCHELL, CARD and HAINES, 1927). *Figure 7.21* shows how the need to increase metabolism on exposure to cold is greatly reduced, as the chick grows older. The body temperature on hatching is lower than that of the adult fowl. It gradually rises to the adult level as the chick becomes adapted to cooler environments (*Figure 7.22*).

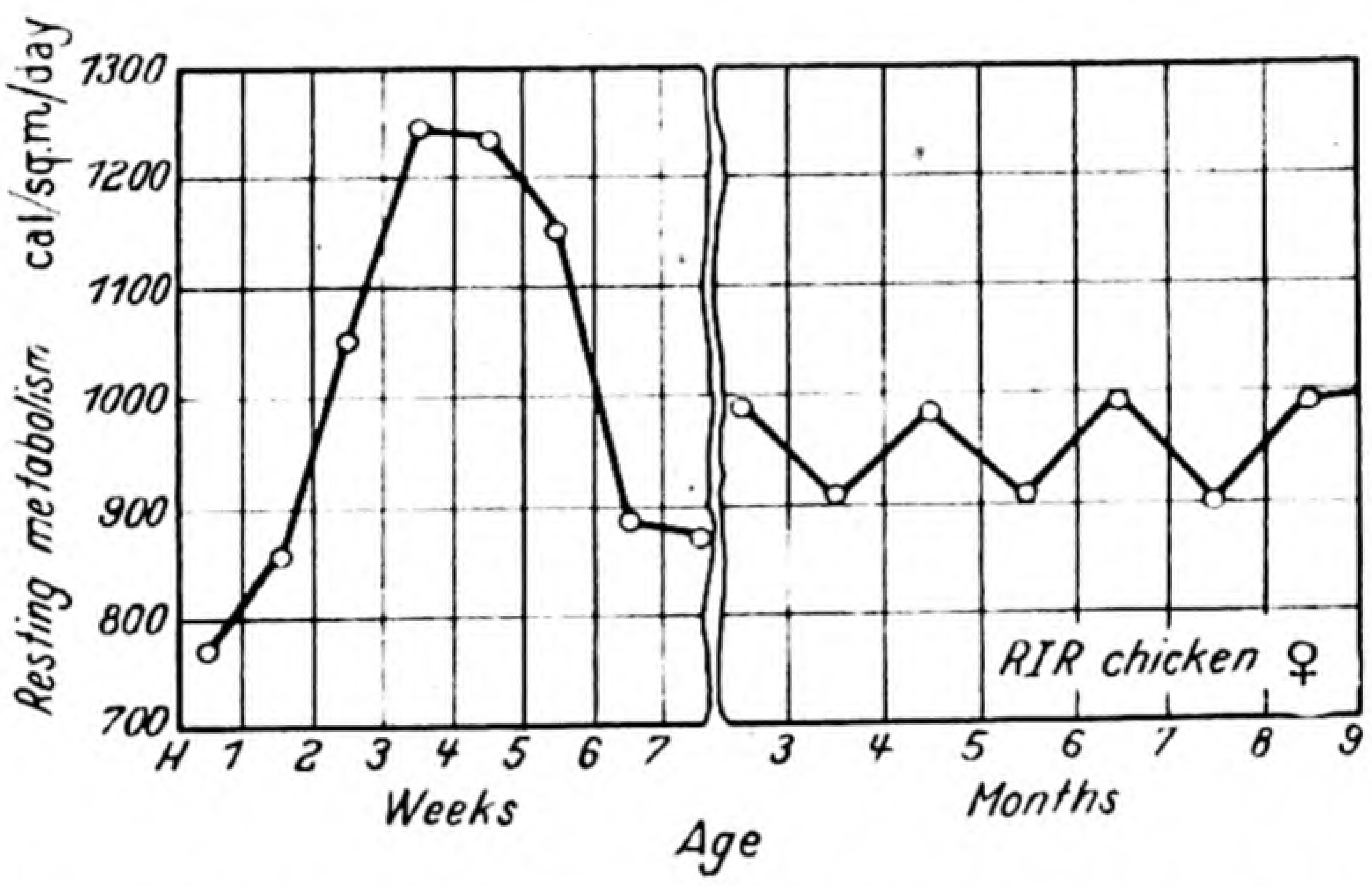

Figure 7.20. Resting metabolism per unit surface area as a function of age in Rhode Island Red chickens measured at temperatures near the critical. Surface area was computed from the equation, surface area in sq. cm. $= 8{\cdot}19 \times (\text{body-weight in g.})^{0.705}$. The resting metabolism was computed on the assumption that 1 litre of O_2 had a heat equivalent of 4·9 Kg. cal. (From Brody, 1945, by courtesy Reinhold.)

The most comprehensive study of heat regulation in an altricial bird is that of Baldwin and Kendeigh (1932) on the house wren. At the time of hatching the chick has no power of regulation. Thus, if it is put in a cool place both body temperature and metabolism fall. If it could increase its metabolism, when chilled, this would be of little help, because there is little heat insulation to retain the heat. Between the third and sixth day the bird gains the ability to keep its body temperature above that of the air, and it is at this time that the feathers begin to develop. At the same time the chick develops the power of increasing its metabolism on exposure to cold, and the basal metabolism, even on a body weight basis, is increased (*Figures 7.23* and *7.24*). Part of the increase of metabolism is due to muscle tremors, the development of which is correlated with temperature regulation and the growth of feathers (*Figure 7.25*). The normal body temperature when the chick is brooded on the nest is shown in

Figure 7.26. It rises during growth like that of the fowl. In the young pigeon the metabolism, which also increases during the early nesting period, is said to be reduced later, like that of the fowl (RIDDLE, NUSSMANN and BENEDICT, 1932), but the measurements were made somewhat below the nesting temperature for young chicks. The reduction does not seem to occur in the house wren (Kendeigh, 1939).

ECTOTHERMIC CONTROL

Ectothermic control in young birds is universal, because the embryos have no means of temperature regulation, yet are not capable of

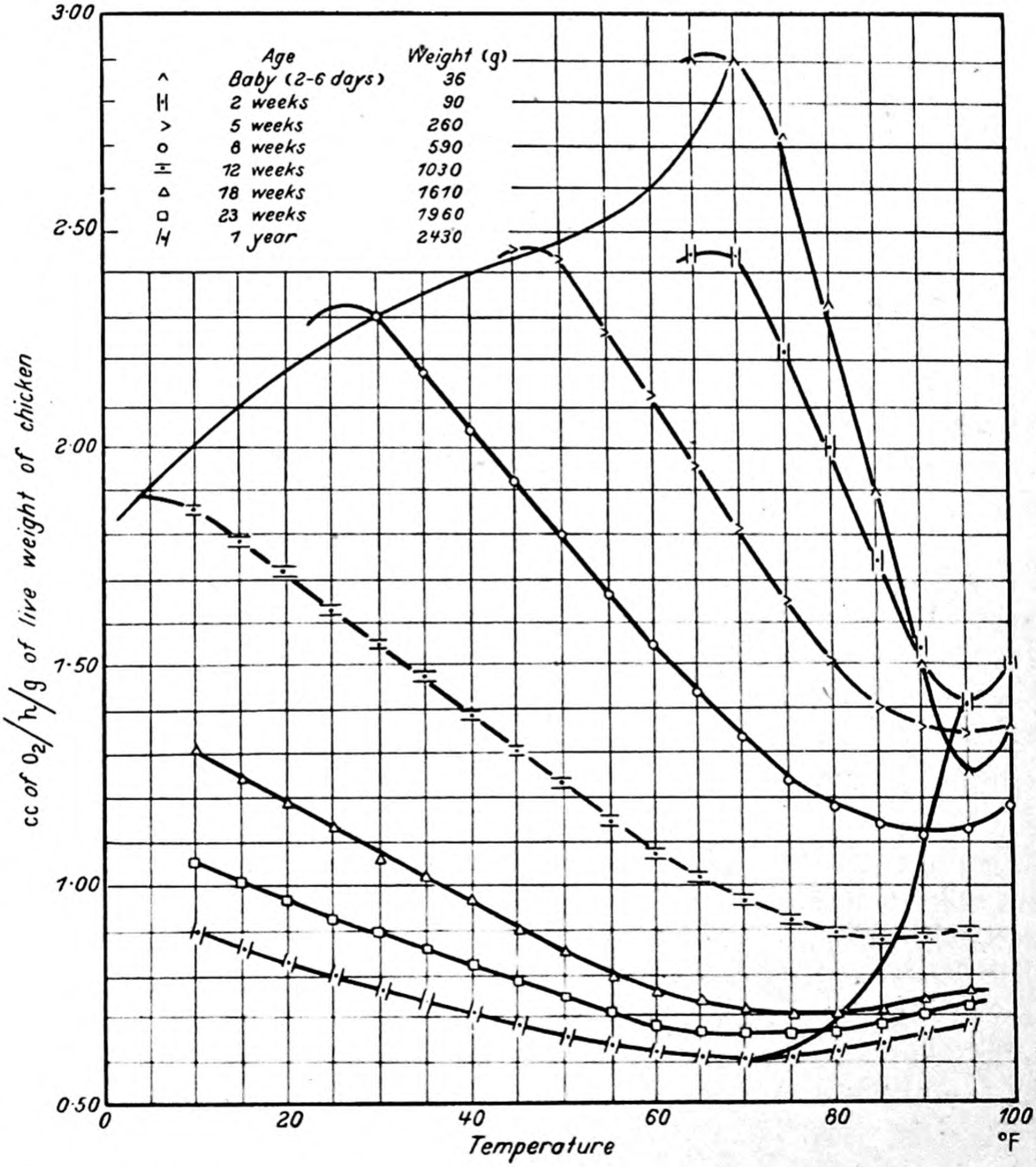

Figure 7.21. Oxygen consumption of fasting chickens at various temperatures; mean of values measured from 8 a.m. to 8 p.m. Mean radiant temperature, same as air temperature; relative humidity 50–60%; air movement slow. (From Barott and Pringle, 1946, by courtesy *J. Nutrit.*)

developing in widely fluctuating temperatures like true poikilotherms. Similarly, the young of most species require external aid to keep them warm. The nesting of wild birds provides the embryo and young with heat insulation, and, in addition, the parents warm them with their bodies.

Agricultural birds by their association with man make use of methods of incubation and brooding provided by the human social organization.

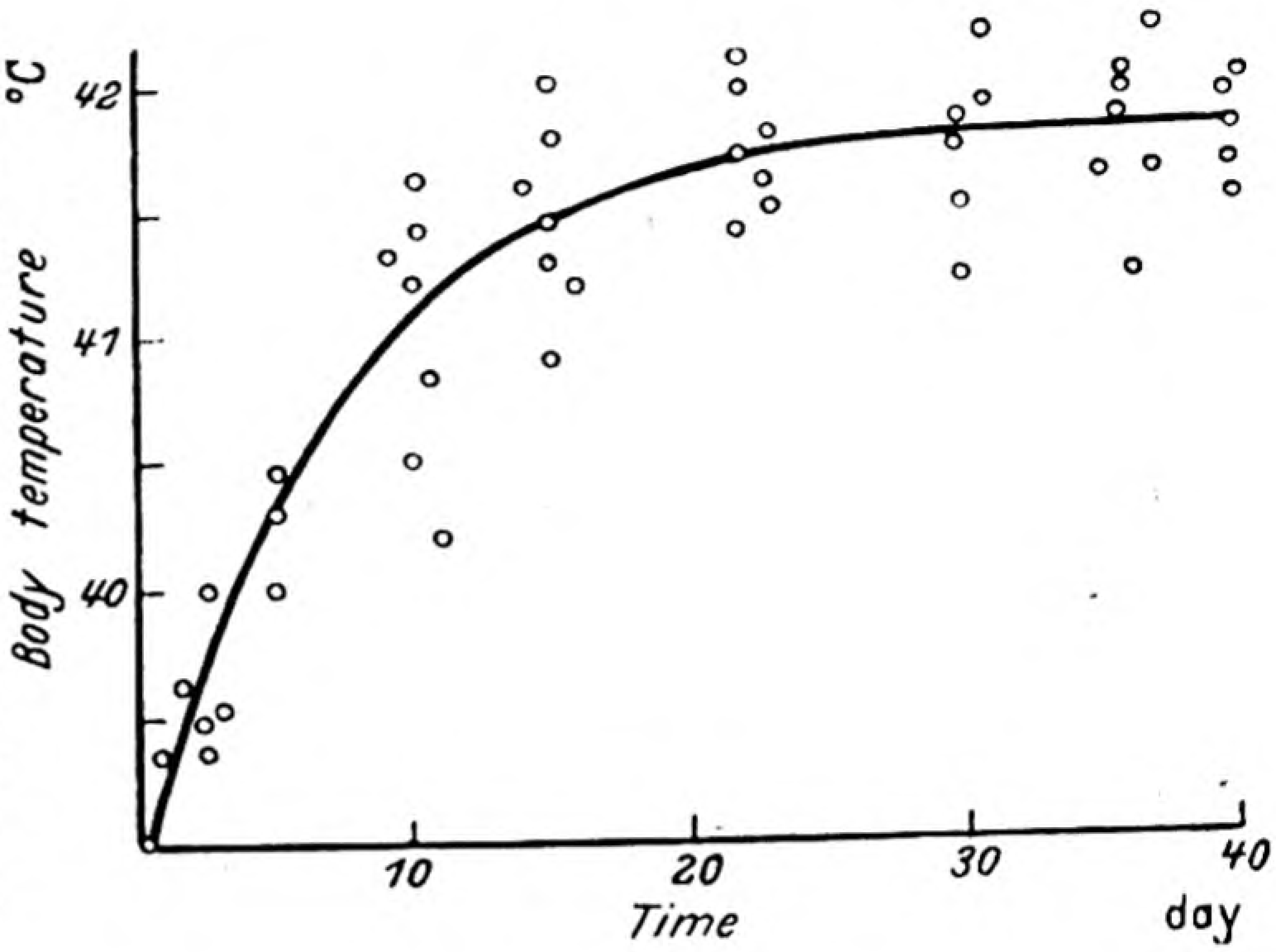

Figure 7.22. The increase in body temperature of chicks from a few hours after hatching to 40 days. The curve represents average temperatures, while the circles give the range of variation. The first two averages were taken with the birds in an environmental temperature of 38–39°C. (100·4–102·2°F.), the remainder at 20–26°C. (68·0–78·8°F.). This progressive development was studied in 40 birds. (From Randall, 1943, by courtesy *Amer. J. Physiol.*)

Incubation

A detailed account of incubation may be found in Taylor's book (Insko, 1949) or Landauer's review (1951), and a few points only will be discussed here. Agricultural birds sit rather closely, and the eggs, being large, retain heat well. They are adapted for incubation at a constant rather than a fluctuating temperature. This makes the design of practical artificial incubators a relatively simple matter, and they have been used for many centuries in China and Egypt. The operation of an incubator to give the maximum possible hatch is not so easy for a number of reasons. First, the determination of the optimal conditions is empirical, and the number of possible combinations of meteorological factors at various stages of incubation is so large, that all the possibilities have not been tested. Secondly, in the cabinet type of incubator no attempt is made to incubate the eggs in their natural environment for engineering reasons, for the air movement is much higher, and there is no temperature gradient through the egg. Moreover, there is some disagreement amongst observers as to the exact conditions under a hen (Eycleshymer, 1907; Lamson and Edmond, 1914; Burke, 1925; Kuiper and Ubbels, 1951). Thirdly, the thermometers, as usually set up in commercial machines, do not give a true picture of the conditions inside. For example, wet-bulb readings are sometimes taken in

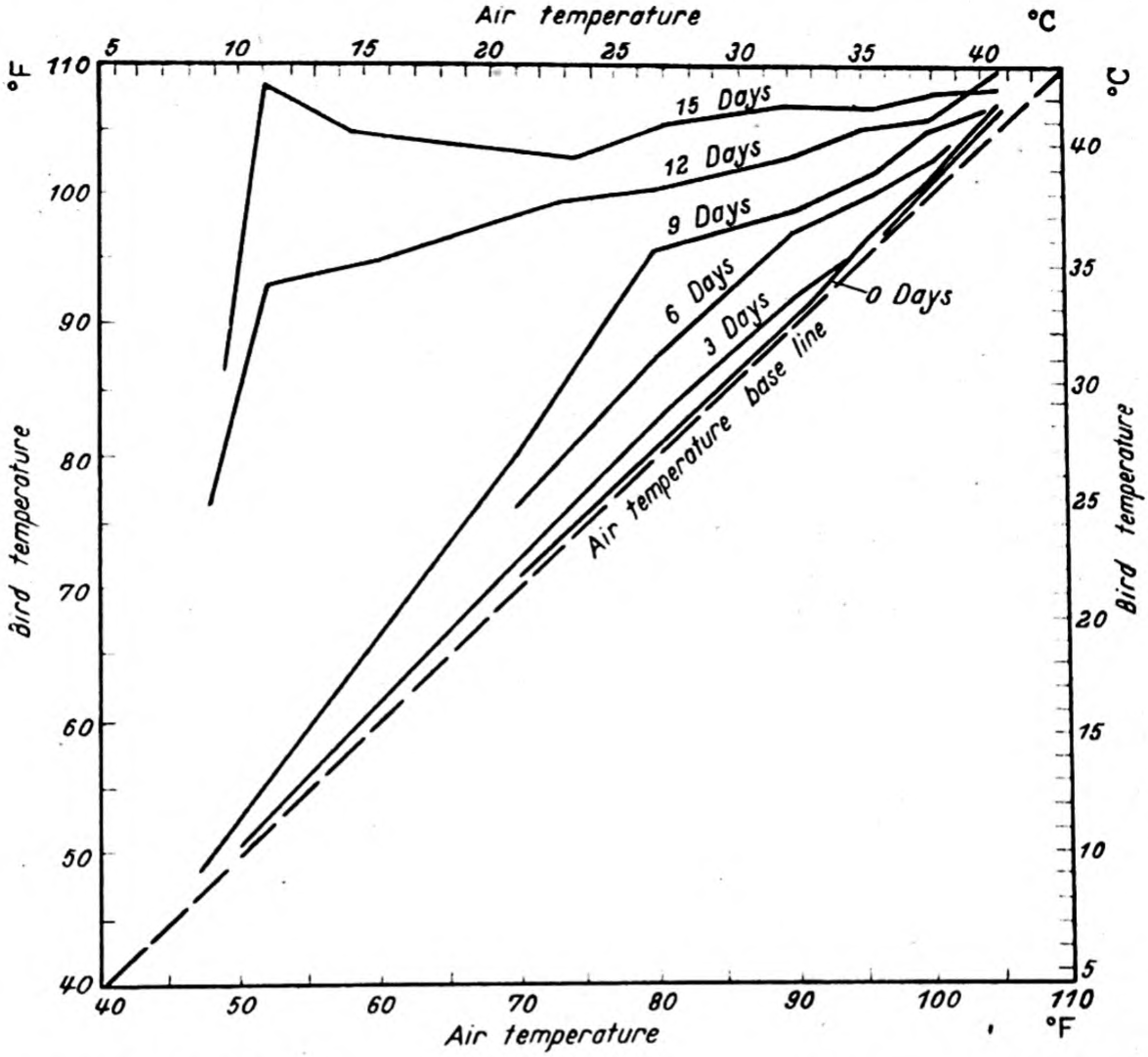

Figure 7.23. Body temperature of fasting young Eastern house wrens after exposure for 3½ hrs. to various air temperatures. Mean radiant temperature close to air temperature ; relative humidity 8–16% ; air movement probably slow. The age of the birds in days is written on the curves. (From Kendeigh, 1939, by courtesy *J. exp. Zool.*)

comparatively still air (THOMPSON, 1952); there may be variations in air temperature in different parts of the incubator, and the wall temperature may not be the same as the air temperature. A farmer, therefore, even if he happens to know what climate an egg prefers, cannot tell if these conditions obtain in his incubator. He, therefore, wisely follows the directions of the manufacturer, who has ascertained that the machine gives a reasonable hatch in his testing shop provided these directions are fulfilled. This empirical system, though at first sight haphazard, usually works quite profitably, but if anything goes wrong it is sometimes difficult to tell whether the incubator, the eggs or the climate of the incubator room is at fault. Where cabinet incubators are used, many hatchery installations now control the temperature of the incubator room. This means that, if the climate of the room is correct to start with, it will remain correct. In addition, the irregularities caused by load sensitivity of the control system or fluctuating wall temperatures are excluded. Probably in the future greater use will be made of giant incubators by hatchery specialists. Owing to the great egg capacity of such machines it is economic to install expensive control systems, exploiting the many recent developments in cybernetic equipment. In addition, better instruments can be incorporated for ascertaining the climate within the machine.

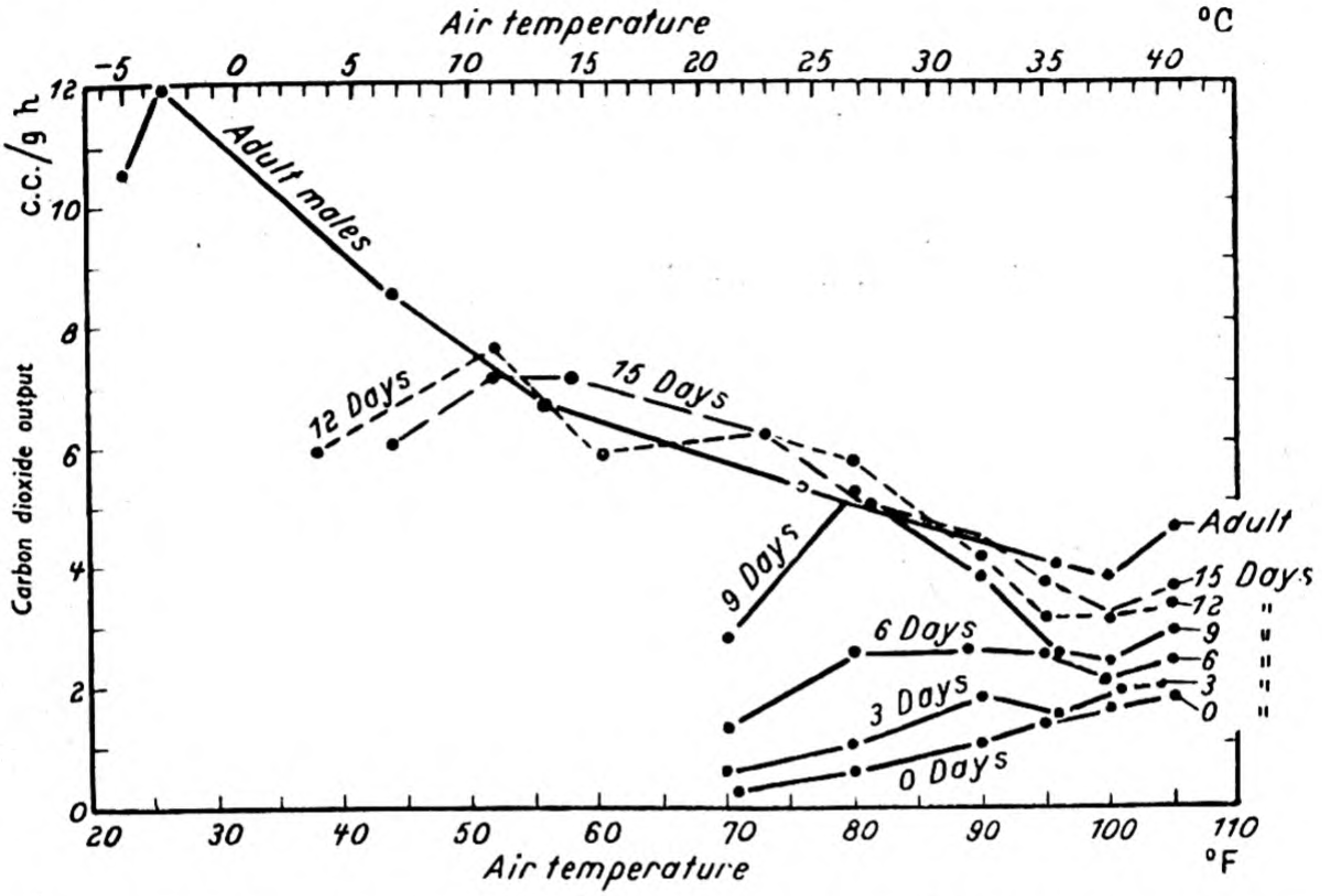

Figure 7.24. Carbon dioxide output of fasting young Eastern house wrens at different air temperatures. Mean radiant temperature close to air temperature; relative humidity 8–16%; air movement probably slow. (From Kendeigh, 1939, by courtesy *J. exp. Zool.*)

It might be thought that the high air movement of cabinet incubators would cause difficulties in hatching. There is some difficulty in getting a good hatch of duck's, quail's and pheasant's eggs (Romanoff, 1938, 1943), and of turkey's eggs in the United Kingdom. High air movement increases heat dissipation during the last week, but hen's eggs, at any rate, will stand a slightly low temperature during this period, though this may not be true for the quail (Romanoff, Smith and Sullivan, 1938; Romanoff, 1938). Whether the evaporation of moisture is affected depends upon whether the egg is like a naked sweating man with a limited wetted area on the surface, or like a man diffusing insensible perspiration through his skin. In the former case a draught would increase evaporation, while in the latter it would make little difference. It seems that the perspiration of the egg is insensible (Romanoff, 1940 ; van Paemel and van Itterbeek, 1951 ; Hutchinson, unpublished observations). The chick once hatched, and before it dries out, is like a sweating man, so that a high air movement might chill it. This may be the reason for the difficulty with some species in cabinet incubators.

Although the eggs of agricultural birds are kept at a fairly constant temperature during incubation, this is not the case with many wild species. *Figure 7.27* shows the temperature fluctuation of eggs of the house wren during natural incubation. The temperature falls considerably each time the parent bird leaves the nest to feed, and rises again when she returns. At night it is comparatively constant. The eggs of this species are difficult to hatch by artificial incubation, perhaps because they are adapted to a fluctuating climate. Before incubation a bare patch appears on the breast and belly of the female (in most species by moulting), so that the heat of her body may be easily transferred to the eggs. There is some evidence of local vasodilatation over this region to raise skin temperature (Baldwin and Kendeigh, 1932).

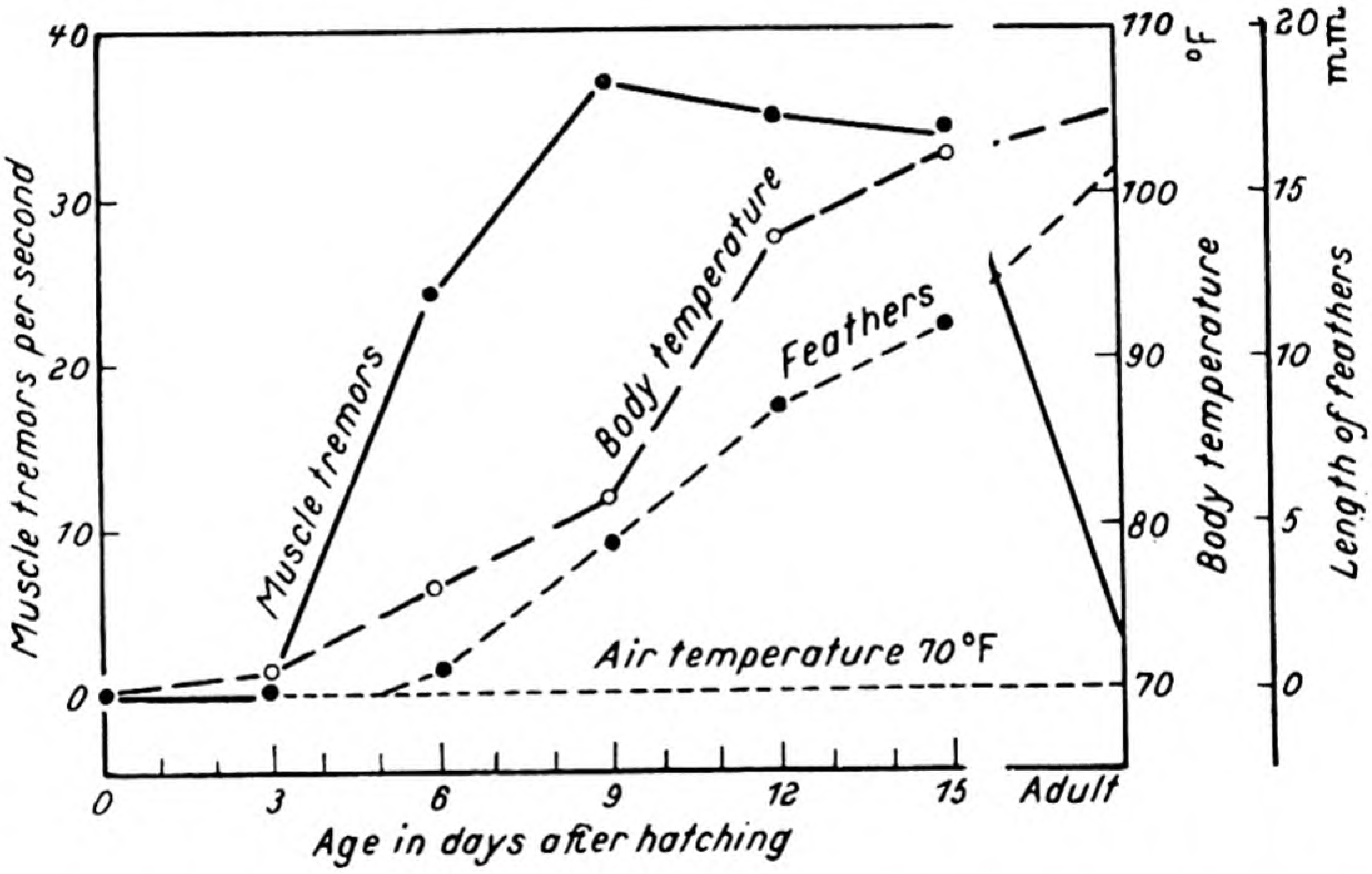

Figure 7.25. Relation of muscle tremors, body temperature and feather development in Eastern house wrens. Observations on body temperature and muscle tremors made at an air temperature of 70°F., not in the normal environment. (From Odum, 1942, by courtesy *Amer. J. Physiol.*)

Brooding

Since the temperature regulation of birds is gradually developed, they require brooding at a high temperature after hatching, and the amount of heat is cut down as they grow older. In the poultry industry the methods of brooding devised by man have practically ousted the natural method, and a great variety of equipment is described in text books on poultry husbandry. Recently infra-red lamps have become fashionable, despite some trouble with toe deformities (Black, Getty and Morris, 1952). They warm the chick mainly by radiation rather than by heating the air around it. The ordinary type of electric battery heater also warms the chick largely by radiation, but the air in the enclosed heated compartment is warm as well. At first sight the infra-red lamp would seem a very risky method of brooding chicks, for there is often no thermostatic control of the heating. Moreover, it is quite impossible to gauge the climate by the reading of a mercury thermometer (*see* page 343). In practice, however, the chicks sit round the lamp in a circle, and control their body temperature by moving towards or away from it, just as adult lizards do by moving into or out of solar radiation. In battery brooders the thermostats often give trouble, and the chicks do not move so freely in and out of the heated compartment, for they sometimes jam the entrance. Curiously enough if chicks are kept at a constant temperature in a climatic chamber, where they cannot regulate their heat by ectothermic means, they grow just as well as, or better than in a battery brooder (Barott and Pringle, 1949; Coates, Hall and Thiel, 1950). It is difficult to gauge the climate in any brooder, so farmers often regulate them by the general behaviour of the chicks.

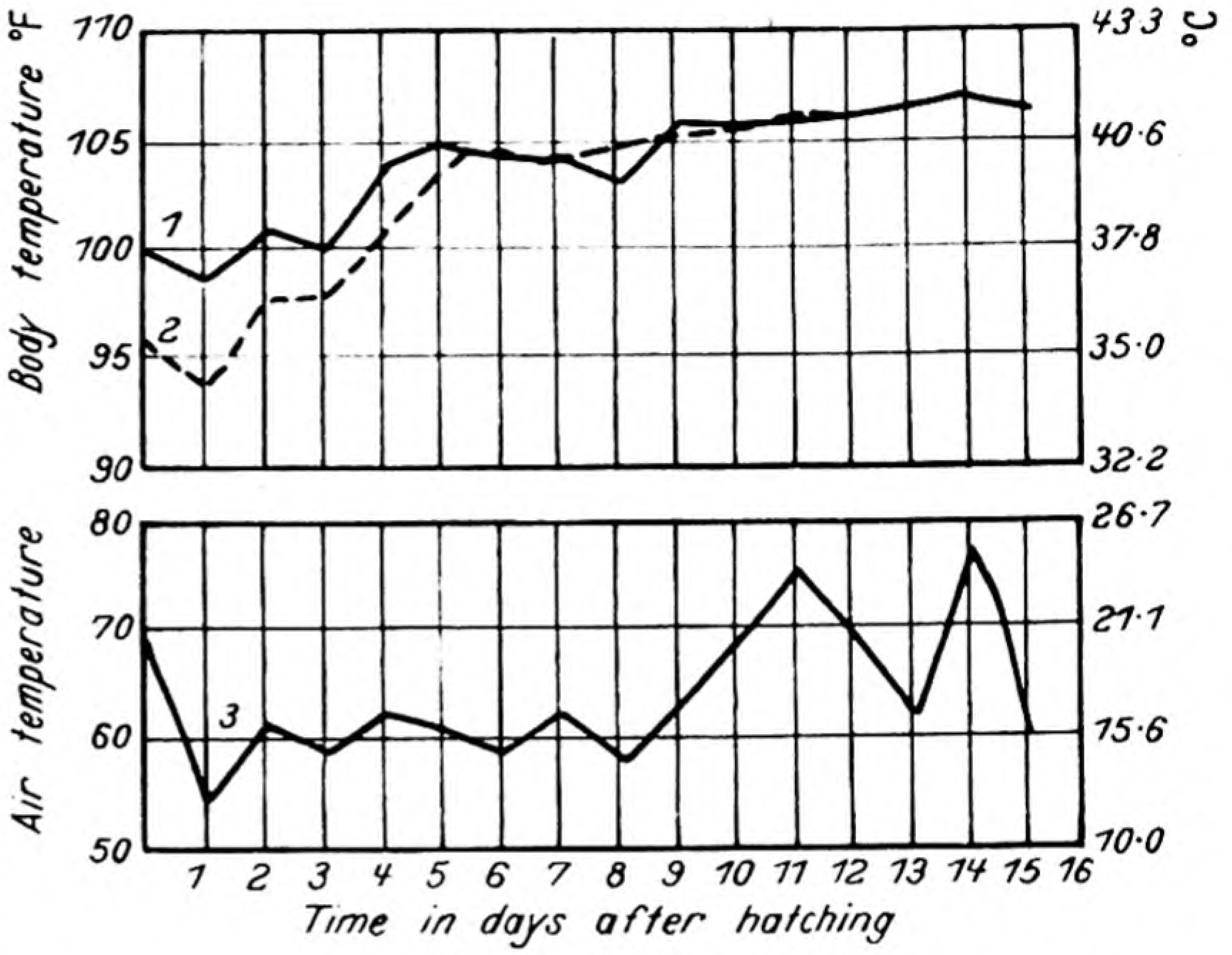

Figure 7.26. Development of body temperature of immature Eastern house wrens in the nest, and correlation with external air temperatures. *1.* temperature of the bird at the end of brooding periods; *2.* temperature of the bird at the end of periods when the female was off the nest; *3.* air temperature. (From Baldwin and Kendeigh, 1932, by courtesy *Sci. Publ. Cleveland Mus. Nat. Hist.*)

If chicks are chilled, they huddle together. This is an ectothermic means of heat regulation, and quite an effective one, for the surface available for heat dissipation is decreased. Kleiber and Winchester (1933) have shown that this huddling saves heat production in a cool environment.

HEAT REGULATION OF BIRDS ON THE WING

Birds fly very long distances without stopping, so they must be able to achieve thermal equilibrium in a variety of climates. One would think that heat regulation during flight would be a subject of unusual physiological interest, but so far it has attracted little attention.

DISSIPATION OF EXCESS HEAT OF FLYING EXERCISE

The metabolism of flight of humming-birds is about six times the resting rate (Pearson, 1950). It may be less in other species, and perhaps small in birds which soar, but in general it must be fairly high. At least three quarters must be dissipated as heat, but it seems a bird would have little difficulty in accomplishing this. The high air velocity past the bird must decrease the insulation of the feathers to some extent. Heat dissipation is further increased by the 'bellows action' of the beating wings (*Figure 7.6*). In addition, the surface area is at its maximum with the wings outstretched, and the under-surface of the wing is poorly feathered. Finally, evaporative cooling must be comparatively high from the strenuous respiration necessary in exercise.

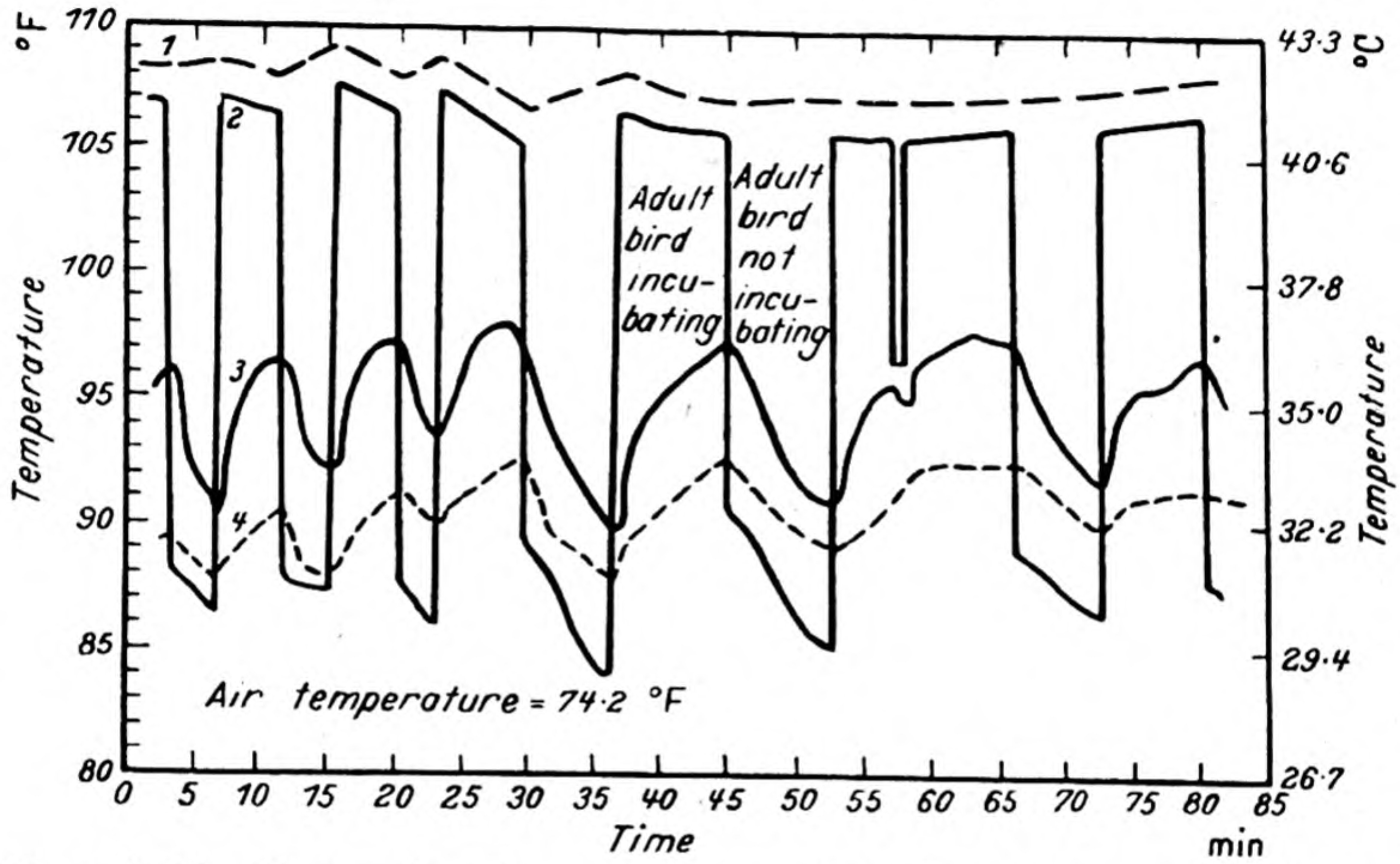

Figure 7.27. Fluctuations in temperature of the Eastern house Wren's egg under normal conditions in the nest. *1.* Body temperature of adult bird; *2.* temperature of the nest just above egg; *3.* egg temperature; *4.* temperature in bottom of nest beneath egg. (From Baldwin and Kendeigh, 1932, by courtesy *Sci. Publ. Cleveland Mus. Nat. Hist.*)

HEAT REGULATION IN DIFFERENT CLIMATES

It is difficult to say anything definite about this. Variation of basal metabolism would have little influence on the heat exchanges, because during flying it is small in comparison with the total metabolic rate. The possibilities of vasomotor control of heat dissipation are obscure. It is known that bats can regulate their temperature by controlling the circulation in the wings (Reeder and Cowles, 1951), but in their case the available area for heat loss is very large.

In flight the respiration of both birds and bats is supposed to be synchronized with the wing beats (KROGH, 1941). One would imagine that the depth of respiration also would be controlled by the mechanical stresses from the flight muscles, so it is hard to see how evaporative cooling can be varied to suit the climate. If this is really true, it is equally difficult to understand how a skylark controls its breath to sing during active flying. ZIMMER (1935) must surely be mistaken in thinking that the trill is caused by the wing beats, for larks can trill both gliding and when on the ground; moreover, the wing beats appear much slower than the trill. Zeuthen (1942) thinks that a flying bird can maintain a higher rate of ventilation than is required for respiratory exchange by contraction of the parabronchial muscles. These would act as variable resistors to prevent over-aeration of the air capillaries and excessive pumping out of carbon dioxide. Perhaps birds have enough control of respiration to influence evaporative loss, but more definite experimental evidence will be required to verify it.

TEMPORARY POIKILOTHERMY

Amongst mammals a poikilothermic phase is widespread ; in this the body temperature is no longer raised above that of the atmosphere. It may be exhibited as a continuous winter sleep, as in the marmot, a broken hibernation with occasional waking periods, as in the hedgehog; or it may be a diurnal as well as a secular phenomenon in bats, whose body temperature even in summer falls during sleep. The necessity for hibernation is sometimes considered to be a consequence of poorly developed heat regulation, and this may well be true. It would, however, be as logical to think of temporary poikilothermy as a specialist adaptation to save food; for the homeothermic way of life is an extravagant one, requiring the burning of some 25 times the amount of fuel that a poikilotherm of the same size needs during inactive and unproductive periods of its life. During hibernation the metabolic rate of homeotherms approaches that of poikilotherms, so that energy expenditure is much reduced. No doubt during activity the ability to maintain the body temperature constant is an advantage in the struggle for existence; but the ability to reduce the metabolism in periods of food scarcity may also be advantageous, especially for animals small enough to hide from their enemies at this time. In bats, which sleep in caves and other safe places, this ability could rationally be extended also to the active season. It is not surprising if the temperature regulation of hibernators is poor, for they are never called upon to maintain homeothermy in unfavourable climates. Their physiological constitution is presumably a balanced one, working on the whole to the advantage of the species. For instance, there may well be a net gain to the hedgehog in swapping some of its insulation for prickles, provided it can hibernate. Whatever its origin, the abundance of bats and hedgehogs around us proves that hibernation is successful.

Birds have much greater mobility than the small mammals. Consequently, many insect eaters like swallows and warblers which breed in high latitudes, migrate in the autumn to warmer climates where their winter-food supply is assured. They have no need to hibernate in order to avoid unfavourable climates or lack of food. Consequently, hibernation is almost unknown amongst birds. There is, however, one exception, the Californian 'poor-will' (*Phalaenoptilus nuttallii*), which has been definitely observed to hibernate by Jaeger (1949). During hibernation its body temperature was about the same as the air temperature.

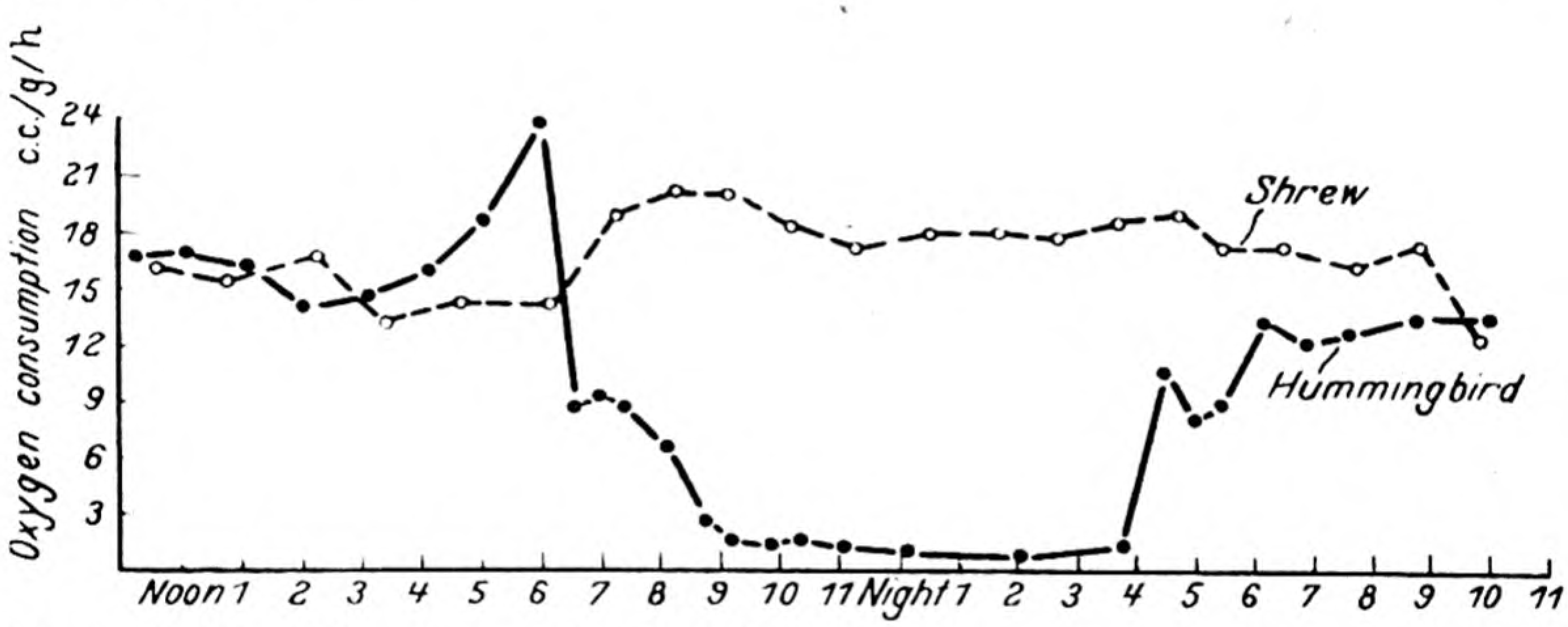

Figure 7.28. The rate of metabolism of a male Anna humming bird (*Calypte anna*) and of a shrew (*Sorex cinereus*) recorded over 24 hrs. (From Pearson, 1950, by courtesy *Condor*.)

Periods of torpidity have been observed in several species (McAtee, 1947), and is common at night in humming-birds (Huxley, Webb and Best, 1939). The body temperature of a female Allen humming-bird (*Selasphorus sasin*) just before waking was found to be about 68°F. at a room temperature of 61°F. *Figure 7.28* shows the metabolism of an Anna humming-bird over a 24-hr. period compared with that of a shrew of about the same size. The environmental temperature was 75°F. throughout the test, and the bird had space to fly when feeding during the day. At night during the period of torpor its metabolism fell to a level far below that of the shrew. The lowest point reached was about 150 kg.cal./sq.m./24 hr., a figure close to that of the hibernating marmot at the same environmental temperature (Benedict, 1938). On account of its nocturnal torpor the daily energy consumption of the humming-bird was only two-thirds of that of the shrew. Thus, it made a considerable saving of fuel in comparison with the mammal. Humming-birds live in equable climates, for the most part in tropical forests, so it is unlikely that poor heat regulation necessitates the torpid period. It is, however, possible that owing to their small size they have difficulty in living without sustenance through the night at the extravagant homeothermic rate of fuel consumption. In tropical climates warming up in the morning would be easier than in colder temperate regions.

Swifts are closely related to humming-birds, and it is an interesting fact that KOSKIMIES (1948) has found that fledglings (*Micropus apus*) exhibit nocturnal poikilothermy during starvation. In bad weather they often have to fast for as long as a week, for the parents leave them and move to other areas until the weather improves (Koskimies, 1950). Nocturnal poikilothermy by its saving in energy expenditure must help the young to withstand hunger.

The pterosaurs may well have had a cycle of body temperature similar to that of humming-birds and bats. The metabolism of flight, even if part of the time were spent soaring, would be high like that of birds. This would mean that the body temperature during activity may have been appreciably above that of the atmosphere. When they rested the temperature would fall again.

Agricultural birds unfortunately do not exhibit a poikilothermic phase. If they did, they might be more economical producers.

LIMITS OF COLD AND HEAT TOLERANCE

BODY TEMPERATURE

Cold

Infant mammals can tolerate a temporary fall of body temperature to lower limits than adults (Adolph, 1951). This is also true for birds. The hen's egg can tolerate 29–30°F. for an hour or so at all stages of incubation (MORENG and SHAFFNER, 1951). Immediately after hatching the lethal temperature rises to 60°F. (*Figure 7.29*). During the first two weeks of brooding it increases further in conformity with the normal body temperature. There is then a slow rise till the value for the adult hen is reached (around 71°F.). The lethal limit for the nestling house wren, an altricial bird, is 47°F., and it rises to 71°F. for the adult (Baldwin and Kendeigh, 1932).

Heat

The ‘ preferred body temperature ’* of active reptiles is close to their lethal high temperature, the upper end of the range being usually within 10°F. of the maximum tolerable without heat collapse; yet they can be cooled temporarily many degrees below without suffering ill effects (COWLES and BOGERT, 1943-4; COLBERT, COWLES and BOGERT, 1945–6). Similarly, the normal temperature of homeotherms is near the upper limit of tolerance. On rapid heating the maximum tolerated by young and adult fowls alike is about 117°F. (Randall and Hiestand, 1939; Randall, 1943; Moreng and Shaffner, 1951). When adults are heated more slowly in climates rather more severe than they can stand, there is danger of heat collapse when the temperature reaches 113°F. (Robinson and Lee, 1946). The same is true for turkeys and domestic ducks. The thermal death point for young and adult house wrens on rapid heating is about 116°F., much the same as for fowls (Baldwin and Kendeigh, 1932). Before incubation the lethal limit for hen's eggs is also the same as for adult fowls. Once incubation has started it is suddenly reduced to 108°F. for the first six days; thereafter it rises rapidly to 114–118°F. for the remainder of incubation (Moreng and Shaffner, 1951).

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* The range of ‘preferred body temperature’ is that which a poikilotherm prefers in carrying out its ordinary activities. If the body temperature rises above, or falls below it, the animal takes avoiding action by ectothermic means, if necessary at the expense of its activities.

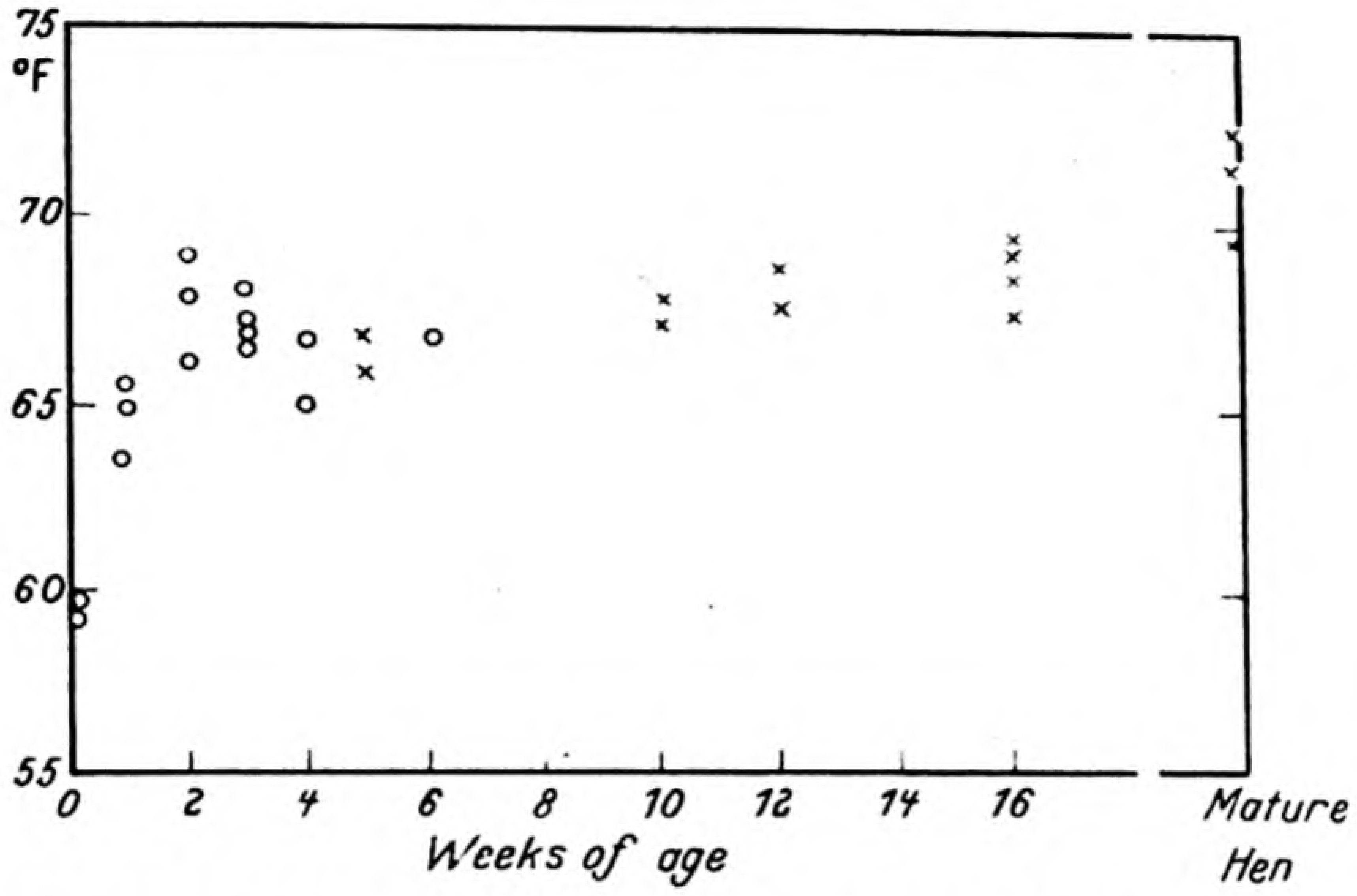


Figure 7.29. Low lethal body temperature of chickens from day of hatch to the mature hen. Each circle represents data collected on 12 birds; each cross, data from individual birds. The birds were exposed to air at – 10°F. The lethal body temperature was that from which 50% of the birds would not recover, when placed in an incubator. (From Moreng and Shaffner, 1951, by courtesy *Poult. Sci.*)

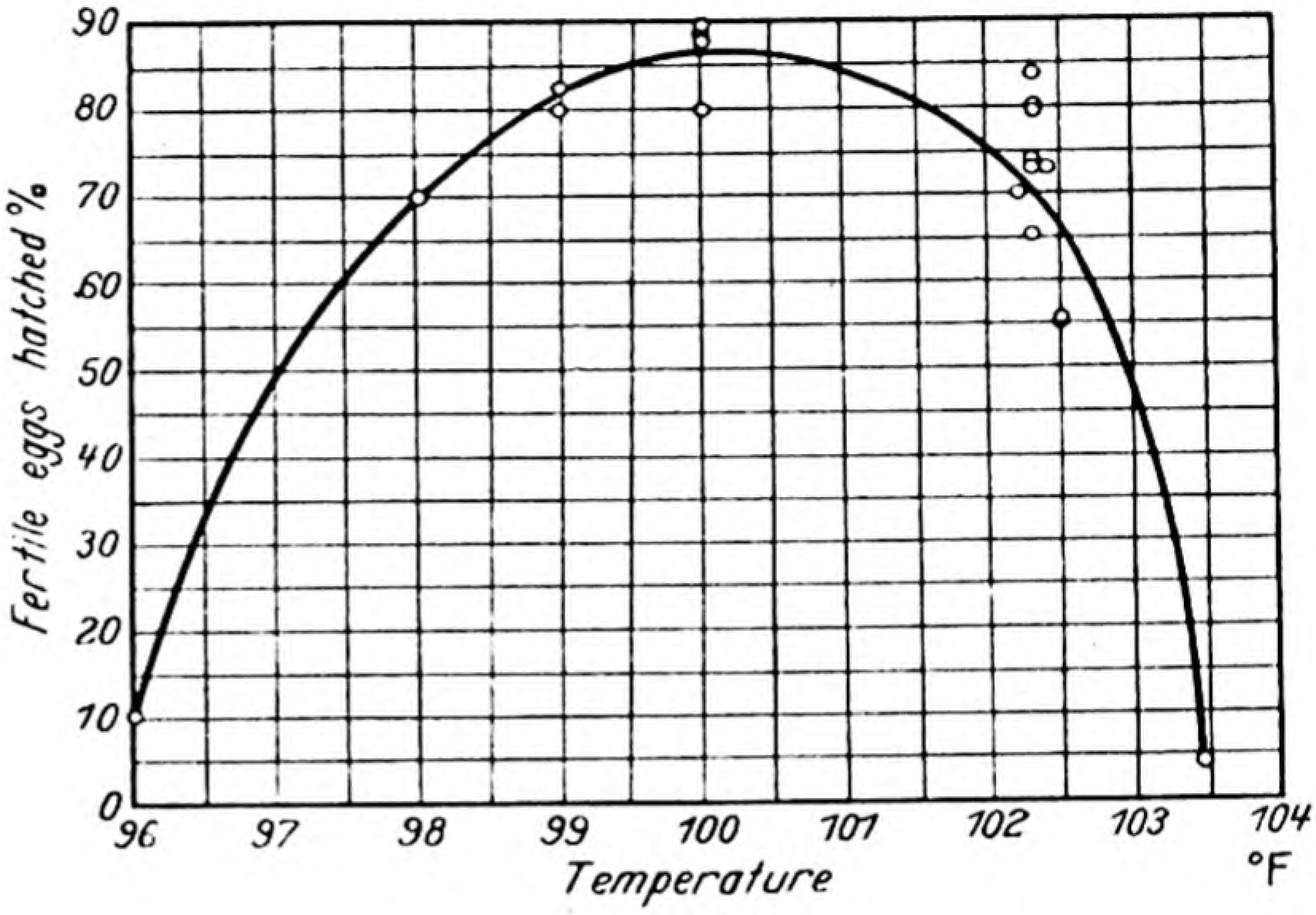
The lethal high temperature for birds is higher than that for mammals and many reptiles in agreement with their high normal body temperatures. There is not yet enough information to say whether the lethal low temperature is also higher than that of mammals, but it is certainly higher than that of reptiles.

Although avian embryos will tolerate extremes of temperature for a short period, they are extremely sensitive to abnormal temperature over the whole incubation period. This is illustrated in *Figure 7.30*. Probably the co-ordination of growth is upset by unsuitable temperatures, although the tissues themselves can tolerate them. Certainly the percentage of monsters at unsuitable incubation temperatures is higher than normal.

CLIMATE

In many instances where climate has been mentioned in this chapter, dry-bulb temperature only is given. This is a quite inadequate specification. In reality the thermal effect of the environment depends on the dry-bulb temperature, the absolute humidity, the air movement and the radiation conditions. The radiation conditions, which in still air are as important as dry-bulb temperature, depend upon the temperature and reflectivity of surrounding objects, the amount of solar radiation and the amount of radiation to or from the sky. In brilliant sunshine in the Arctic, temperatures over 120°F. have been measured with a black-bulb thermometer sensitive to radiation, when the air temperature, taken with a shielded thermometer, was below freezing (SIPLE, 1949). Under these conditions, if a farmer looked at the black-bulb thermometer only, he would expect his fowls to die of heat stroke; if he happened to see the shielded instrument, he would consider hypothermia the greater danger. Thus, the importance may be seen of integrating the various meteorological factors which specify climate, and this has long been realized by workers in human physiology. The effective temperature nomogram (YAGLOU, 1949) integrates the dry-bulb and wet-bulb temperatures with the air movement into a single scale expressing the thermal effect of the environment, and this has been modified and extended by later workers. It must on no account be applied to farm animals owing to the great difference between the heat regulating systems of men and other animals. Because the scale was originally derived from the subjective impressions of men, it follows that a farmer cannot rightly assess the comfort of his hens from his own subjective feelings. It is, therefore, important that similar nomograms should be prepared for the various types of livestock. Yet, armed with a scale of this kind a farmer is by no means out of the wood. The nomogram for man is simple, because

Figure 7.30. Effect of temperature of incubation on the percentage of fertile eggs hatched; mean radiant temperature, same as air temperature; relative humidity 60%; air movement about 12 cm. per min.; 0_2, 21%; CO_2, 0·5%. (From Barott, 1937, by courtesy *Tech. Bull. U.S. Dep. Agric.*)



it is meant to apply to relatively simple indoor situations; but fowls in the field can be in micro-climates, which are difficult to evaluate without surrounding the birds with a whole physical laboratory (*Figures 7.18* and *7.31*).

Human comfort is sometimes assessed by measuring the heat dissipated from a physical model of a clothed man. BERGONIÉ (1904 a,b) constructed the father of these ' artificial men '. Amongst his numerous progeny* was a bastard brood of pigeons and fowls, which GIAJA (1931) used for pilot experiments upon the insulating value of plumage. These instruments could be exploited further to integrate roughly the effect of air temperature, air movement and radiation, but not humidity, in the field. For various reasons the precision attained would not be high, but to achieve the same accuracy by ordinary physical observations would require many complex measurements and calculations. Moreover, the object of an assessment of climate is to express it in a simple way, not as a number of complex physical formulae.

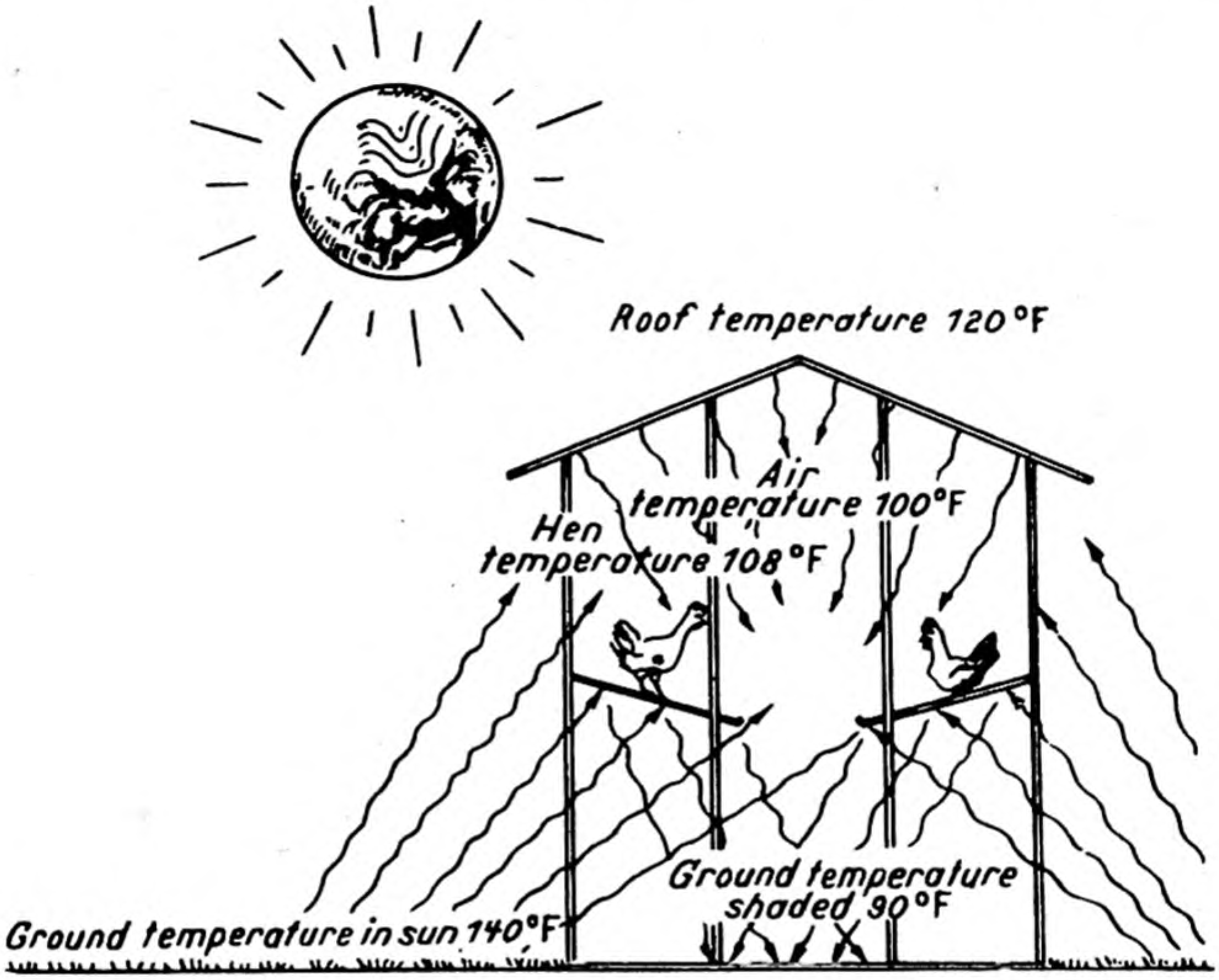


Figure 7.31. Complex thermal situation in a battery laying house. The arrows represent the passage of radiation. (From Wilson and Houck (undated), by courtesy Univ. Calif. agric. Exp. Service.)

Cold tolerance

This depends upon the climate to which the species is adapted. In general, birds are able to live without ectothermic protection in colder climates than mammals of equivalent size, for in winter small arctic mammals spend most of their time in well insulated nests, whilst arctic gulls and snow buntings can live in the open (Scholander *et al*, 1950a). Similarly, fowls are more tolerant of extreme cold than rabbits of the same size (HORVATH and his colleagues, 1948). The reason for this difference is either that feathers are superior to fur as an insulator, or that small mammals have underground shelters more readily available to them than birds. Small birds of the temperate zone, such as the greenfinch, house sparrow, goldfinch and skylark will maintain homeothermy for about an hour at – 25°F. with a low air movement. The fowl will tolerate nearly – 58°F., while the pigeon is even more cold resistant (GIAJA and GELINEO, 1933). Homeothermy in the turkey is broken at – 40°F., the duck will tolerate down to – 148°F., while the domestic goose can actually maintain its normal temperature for 3½ hr. at an environmental temperature of minus 130–152°F. A temperature of – 238°F. proves too much for it (Giaja and Gelineo, 1936). Pigeons and ducks are extremely resistant to the combined effects of cold and starvation. For example, fasting pigeons were able to survive 48–144 hr. exposure to – 40°F., while ducks could survive 7–16 days in these conditions (STREICHER, HACKEL and FLEISCHMANN, 1950). Fowls may get frost-bitten combs on any night when there is a frost, if their combs are large and they live in houses with poor roof insulation.

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* Homunculus (CANNY and MARTIN, 1939), Jernhenrik (PEDERSEN, 1948) and the transatlantic race of copper men are the most celebrated.

Heat tolerance

In the field.—Study of the mortality of fowls in heat waves in the north eastern United States indicates that there is danger of heat stroke whenever the maximum temperature exceeds 100°F. (Hutt, 1938; Fox, 1951). However, in really hot countries, such as India, they appear to be able to withstand temperatures over 110°F., and heat stroke is not an important cause of mortality (IYER, 1952). The amount of acclimatization to heat which Hutchinson and Sykes were able to induce was not enough to account for this difference between American and Indian fowls, though of course it may not have been the maximum which a fowl could achieve in India. Another possibility is that breeds from the temperate zone get genetically adapted to hot environments by selection. This could happen much more rapidly with fowls than with the large farm animals, because a new generation is raised every year, and the selection differential applied is large. It is probable that the micro-climates, inhabited by fowls in hot countries, are more favourable than the readings of instruments at local meteorological stations would indicate.

In laboratory experiments.—This depends upon acclimatization (page 321, and on breed as explained later. LEE and his colleagues (1945) found that the maximum temperature that could be tolerated by unacclimatized hens for 7 hr. lay roughly between 100° and 105°F. The air movement was about 100 ft./min. and the humidity varied in different tests. Radiation conditions are not recorded. The fowls had access to water, in which they could dip their combs and wattles. Temperatures above 85°F. usually produce a rise in rectal temperature, but this depends on the heat tolerance of the particular fowl, its state of acclimatization *etc*. Above this critical value the body temperature rises rapidly with increase of environmental temperature. This is shown in *Figure 7.32* for unacclimatized Brown Leghorn cocks and laying hens. It may be seen that the cocks were more heat tolerant than the hens, but this may not be true for other breeds and flocks (Fox, 1951).

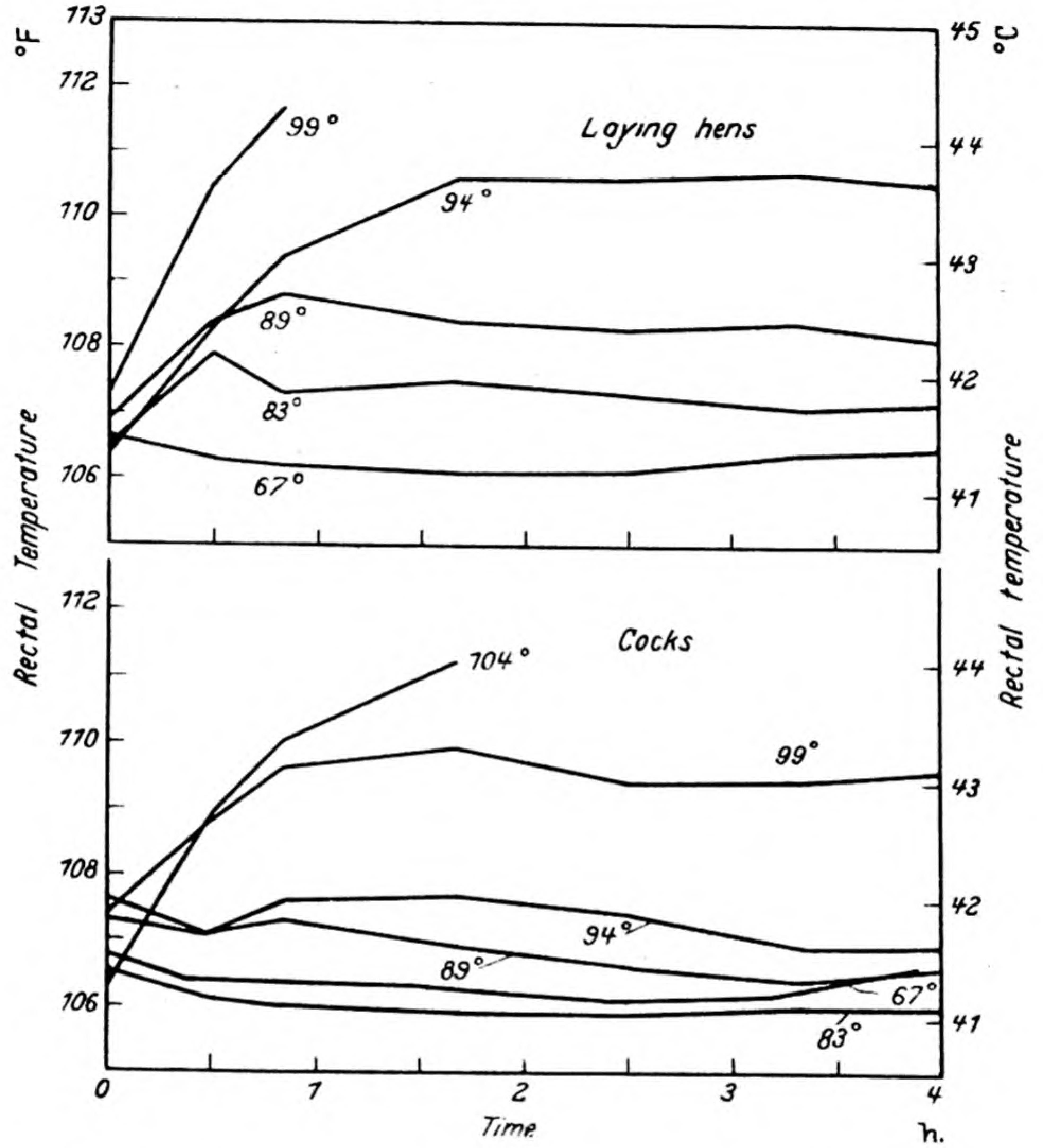

Figure 7.32. Rectal temperature of unacclimatized Brown Leghorns on exposure to hot environments. The humidity was 28 mm. Hg vapour pressure and the air movement about 20 ft. per min. in all tests. The air temperature is marked on the curves in °F. The mean radiant temperature was within 1°F. of this. There were 3 birds of each sex. (From Hutchinson and Sykes, unpublished observations.)

Effect of humidity.—Figure 7.33 shows the combined effect of temperature and humidity on rectal temperature. The effect of humidity was not very consistent in the experiments depicted, but was clearly not large. Reference to the nomogram of effective temperature for man will show a marked contrast between men and birds in this respect. Humidity is only important in dry-bulb temperatures above 90°F., because intense polypnoea does not begin until about this temperature. The author found that for acclimatized Brown Leghorns a dry-bulb temperature of 99°F. with a humidity of 28 mm. Hg vapour pressure and low air movement was roughly equivalent to one of 103°F. at 11 mm. humidity. Now 28 mm. is about the maximum humidity

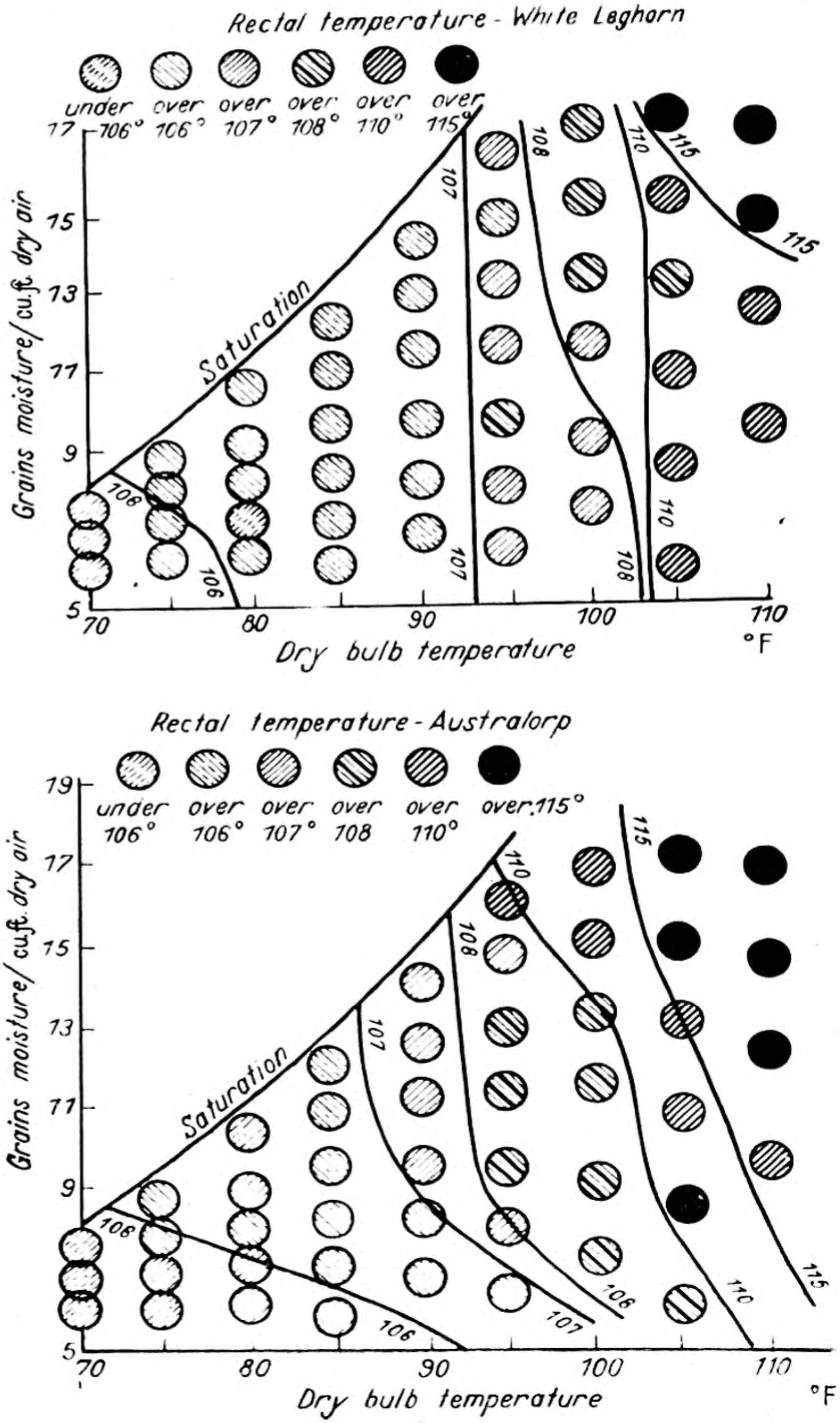

Figure 7.33. Temperature-humidity grid for rectal temperature of unacclimatized hens. Average rectal temperature during 7-hr. exposure; air movement 100 ft. per min.; radiation conditions not recorded. The width of the range of humidity covered is the maximum found in nature, but the highest humidity is higher than the highest natural humidity. Similarly, the lowest is higher than the lowest natural humidity. (From Lee *et al*, 1945, by courtesy *Poult. Sci.*)

which fowls encounter in nature, while 11 mm. is within the range of desert climates. So it would be reasonable to deduce that in severe heat stress a change of humidity from the highest to the lowest found in nature (*ca.* 5 mm.) is equivalent to only about 5°F. dry-bulb temperature. The importance of this fact in the cooling of poultry houses by evaporative devices has already been mentioned.

Effect of air movement.—At dry-bulb temperatures above the body temperature air movement tends to reduce heat dissipation by increasing the flow from the environment through the skin into the body of the bird. This is because air movement reduces the insulation of the surrounding air, and may also reduce that of the feathers. At air temperatures close to the body temperature air movement will make little difference, because most of the heat will be dissipated by evaporation from the lungs and respiratory passages, and there will be little heat transferred through the skin. At lower temperatures, say below 100°F., air movement may be important, but there is no definite information on the subject. Lee *et al* (1945) could demonstrate little effect over a range of 20–300 ft./min. This may have been because they only used two dry-bulb temperatures, one of which was too low to give an appreciable elevation of rectal temperature, and the other so high that there would be little heat passing through the skin. However, it should be mentioned that, if the feathers are windproof, it may be calculated that the air movement will not greatly affect heat dissipation.

Breed differences in heat tolerance in the field and laboratory.—There is a good deal of evidence that the light breeds can withstand heat better than the heavy breeds. For example, Hutt (1938) found that in a heat wave at Cornell the mortality of S.C. White Leghorns was less than that of Rhode Island Reds or Barred Plymouth Rocks. The birds appear to have been housed indoors. Had they been in the open, the White Leghorns would have had an additional advantage, because their feathers would reflect the radiation in the visual spectrum. Lee and his colleagues (1945) in 7-hr. laboratory experiments found that Australorps and Rhode Island Reds were consistently bad performers, while White Leghorns were more heat tolerant. The performance of Minorcas and White Wyandottes was intermediate. Brown Leghorns were intolerant of hot dry climates, but could tolerate hot humid climates better than the other breeds. If this were confirmed, it would indicate that the effect of humidity would be less for the author's Brown Leghorns than for other breeds (*see Effect of humidity*). Wilson (1949) found that the body temperature of S.C. White Leghorns was lower than that of Rhode Island Reds during continuous residence in artificial hot climates. In addition, the egg production of the Leghorns was less affected by heat. It is the general experience of Indian Government Poultry Stations, that light breeds are less susceptible to heat stroke. Only one author has reported superior heat tolerance for a heavy breed. Fox (1951), measuring survival time at a dry-bulb temperature of 108°F. and a high humidity, found that White Plymouth Rocks survived longer than S.C. White Leghorns.

Heat tolerance of chicks.—Baby chicks, as would be expected, are more heat tolerant than adult fowls. This is apparent from *Figure 7.21*, where it may be seen that metabolism experiments could be performed at higher temperatures with chicks. The maximum which day-old chicks can withstand in a chickbox is of the order of 106°F. (Wilson and Edwards, 1950). New Hampshire chicks are less heat resistant than White Leghorns (Wilson and Plaister, 1951). The males of the New Hampshire breed are slightly less tolerant than the females, but this is not the case for White Leghorns. Although chicks can withstand heat better than adult birds, overheating is just as important from the farmer's point of view, especially during shipment. This is because the metabolic heat of the young birds raises the temperature in the box considerably above that of the outside air. Whenever the environmental temperature rises above 90°F. there is danger of loss from overheating in chick boxes. High summer temperatures above 90°F. also reduce the rate of gain of growing stock (Kempster, 1938). Better growth may be secured if the chickens are made to feed at night (Heywang, 1946a).

Heat prostration.—Heat prostration of fowls is analogous to heat stroke in man, but not to the various syndromes classified as heat exhaustion. The condition is caused by damage to the brain. The fowl becomes ataxic at a rectal temperature around 113°F. and soon afterwards is prostrated. The respiration becomes laboured and slower, and eventually gasping. Death, which follows quickly, is probably due to asphyxia causing heart failure (Randall, 1943). Once a fowl becomes prostrated, it must be revived immediately or death will ensue.

Figure 7.34 gives a general idea of the effect of temperature on the laying hen. It is not intended to be accurate, but is useful for practical purposes.

EFFECT OF CLIMATE ON THE SEASONAL RHYTHM OF EGG-PRODUCTION

It is difficult to separate the effects of temperature and day-length on seasonal production, because in nature they are closely correlated. For simplicity it has been assumed throughout this chapter that the winters over much of the temperate zone are cold enough to reduce production. This is the opinion of practical farmers, and the success of the deep litter system is ascribed to its heating property as well as to the nutritional benefits obtained. But it must here be admitted that this is a subject on which science speaks with many voices (Smith, 1930; Bruckner, 1936; Lee and his colleagues, 1937; 1939; Gutteridge *et al*, 1944; Wagener, 1949; Warren and his associates, 1950). In Warren's experiments, perhaps the most careful so far made, both the cold of winter and the heat of summer were found to reduce production slightly in Kansas. Nevertheless, the available evidence suggests that in the temperate zone day-length is far more important than temperature in controlling the seasonal rhythm of production.

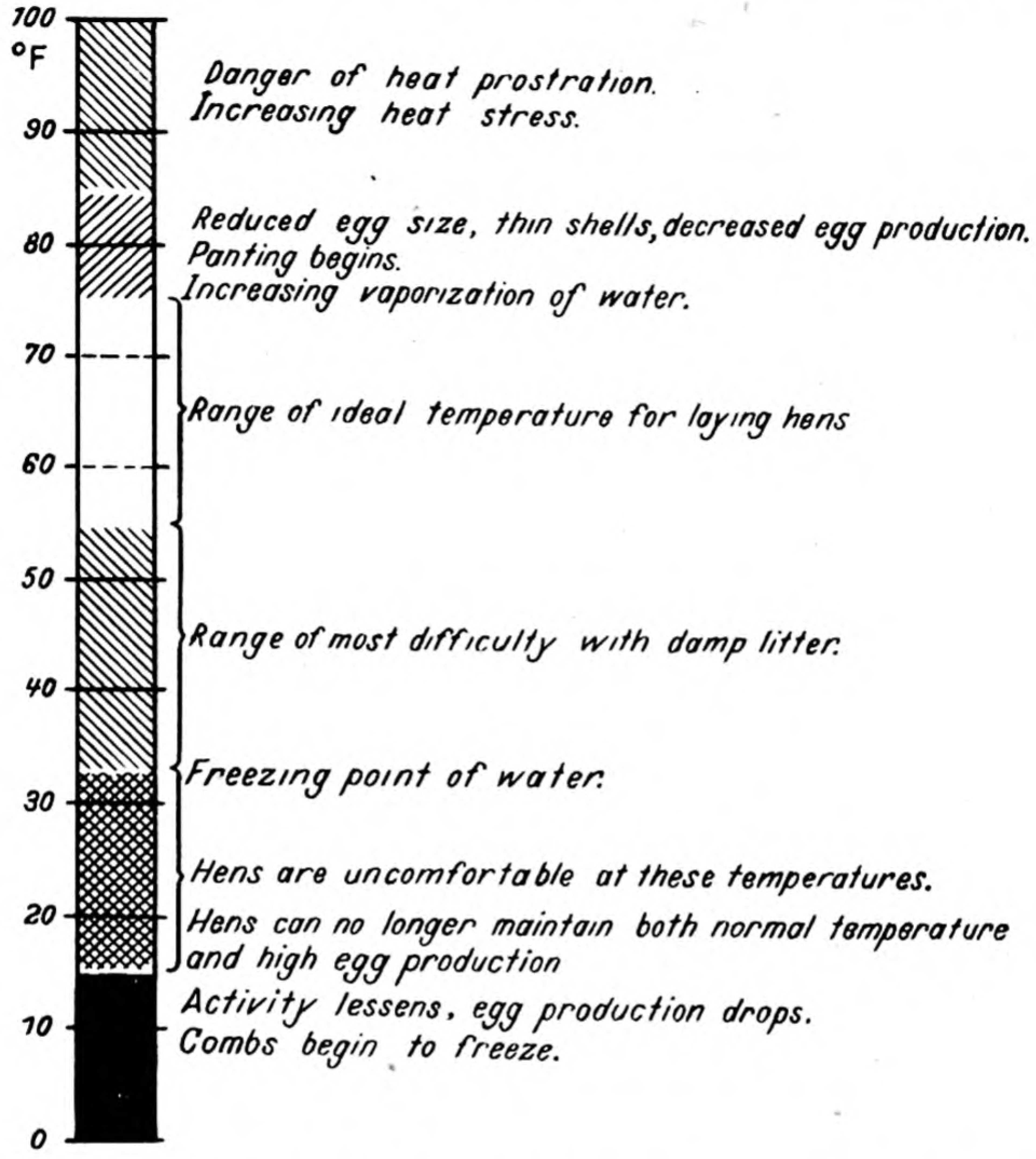
100
°F
90
80
70
60
50
40
30
20
10
0
Danger of heat prostration.
Increasing heat stress.
Reduced egg size, thin shells, decreased egg production.
Panting begins.
Increasing vaporization of water.
Range of ideal temperature for laying hens
Range of most difficulty with damp litter.
Freezing point of water.
Hens are uncomfortable at these temperatures.
Hens can no longer maintain both normal temperature and high egg production
Activity lessens, egg production drops.
Combs begin to freeze.

Figure 7.34. Showing how temperature affects the laying hen. (From Card, 1952, by courtesy Lea & Febiger.)

In the sub-tropics and tropics the position is not so clear, because experiments with controlled temperature and lighting have not yet been carried out to investigate separately the effects of each. It is true that Wilson (1949) has shown that at 90–100°F. egg yield is reduced, but these experiments were made without the normal diurnal rhythm of temperature which gives the birds relief from the heat at night. However, farmers find that production drops during the hot weather, and attribute this to the heat. As one passes from the temperate zone to the Equator, the seasonal change in day-length is progressively decreased. In latitudes below 30° the seasonal variation in production is also reduced until in equatorial climates it becomes small (WHETHAM, 1933). It might be argued from this that day-length is the most important seasonal factor. However, the seasonal change in temperature, which is large in the sub-tropics is also greatly reduced as one passes to the Equator, so this argument is not valid. The complexity of the situation may be seen from *Figure 7.35*, which illustrates the wide variation in time of peak production, which can be observed in the Northern hemisphere. In Hawaii the maximal temperature is seldom over 85°F., and the seasonal range only about 8°F.; there is little change in day-length. The curve of egg production appears to be an endogenous one, since there are no adverse conditions of temperature or day-length. It may be seen that there is a peak early in the laying season. In Izatnagar, at much the same latitude, the pullets mature more slowly, presumably on account of high summer temperatures, which often exceed 110°F. When they do begin to lay, they quickly reach their maximum rate like the Hawaiian birds. However, during summer, production drops much more rapidly than in Hawaii, and this may be an effect of high summer temperatures, which in northern India occur chiefly in May and June. In the high latitude of Ayrshire the peak of production is about

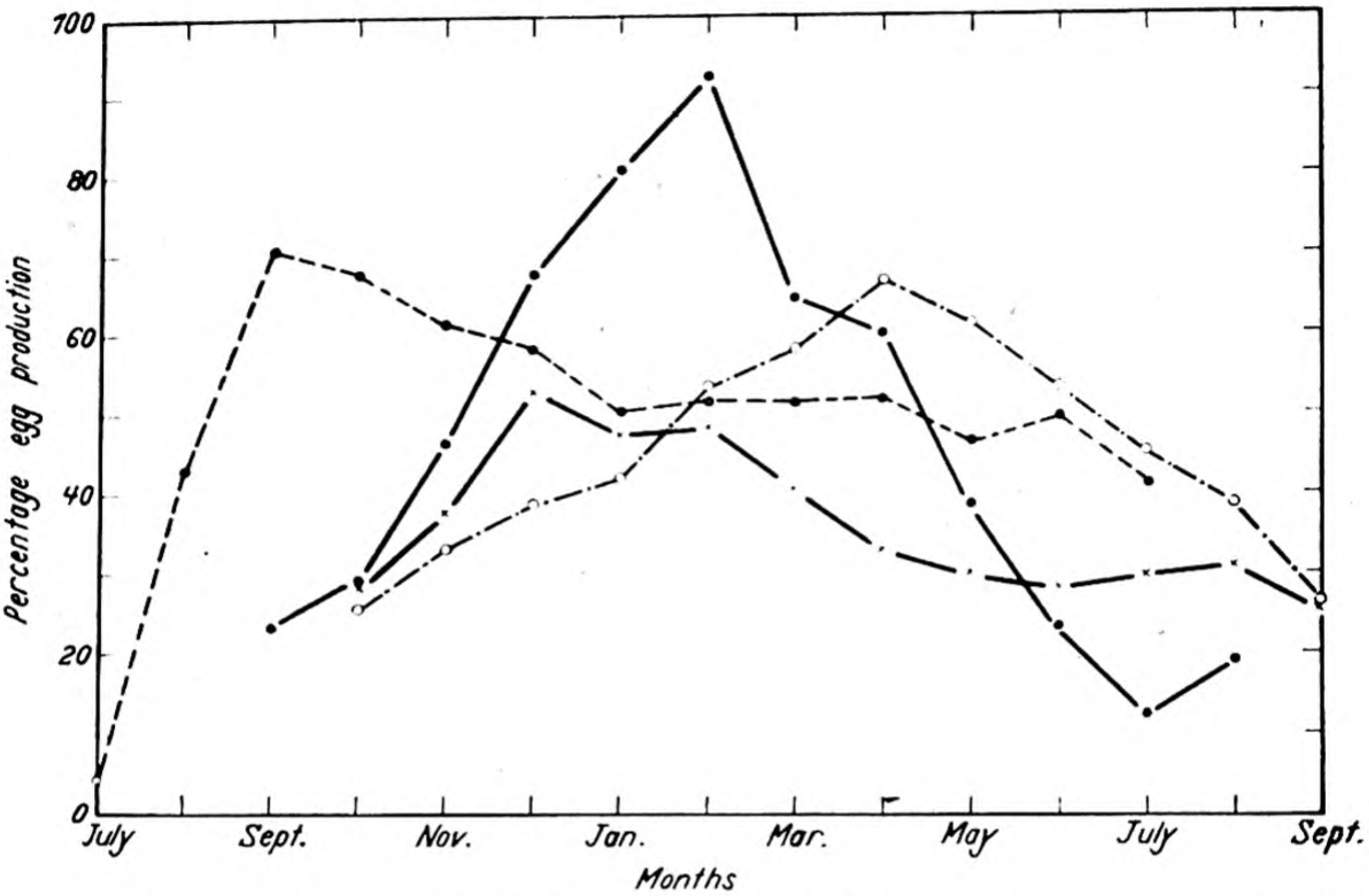

Figure 7.35. Seasonal variation in egg yield of pullets. .- - -. Mean of 4 strains of New Hampshires housed in batteries in Hawaii; hatched, March 3. Warm oceanic climate; Lat. 21°N. (After Rosenberg and Tanaka, 1951a.) .——. Various breeds at Izatnagar, India ; semi-intensive system, hatched in January. x——x Desi breed at Izatnagar; semi-intensive system ; hatched December–March; mean of 5 years. Very hot summers, cool winters; Lat. 28°N. (Data from Indian Veterinary Research Institute, 1951; Iyer, 1949; 1952.) . -. - o Rhode Island Reds in Ayrshire, Scotland; semi-intensive system without winter lighting; hatched in March. Cool temperate climate; Lat. 55°N. (Data supplied by Mr. W. W. Taylor.)

7 months later than in Hawaii. This is due to the unfavourable day-length in autumn and winter, and to a smaller extent perhaps to inclement weather. It should be emphasized that the interpretation of field data must in general be tentative owing to the many variables which can affect production, such as breeding, management, date of hatch and nutrition. The variability of such records is well illustrated by Whetham (1933). Perhaps the safest conclusion is that we know less than we ought about the elementary biology of the hen, and that it is important to make carefully controlled experiments in climatic chambers.

The Hawaiian type of curve, with its autumn flush, is an attractive one from the point of view of a farmer in the temperate zone, and it would seem that little further research need be done to produce it economically. However, the problem may be a little more subtle than it appears; for instance, in high latitudes it may be as important to restrict the day-length to 12 hr. or so during the rearing season, as to give the pullets warmth and extra light in winter.

There is no evidence that the reduction in thyroxin secretion on acclimatization to heat affects production, for a high egg yield can be maintained in climates warm enough to induce it. The fall in production in hot weather is more probably due to the general physiological stress imposed by extreme climates. It has been found that in Hawaii, pullets, kept on wire floors in open shelters, show a drop in production in autumn and winter while birds maintained in confinement on litter, exhibit a curve of production like that in *Figure 7.35* (ROSENBERG and TANAKA, 1952). The fall is attributed to strong trade winds in open shelters, but the authors do not say whether it is buffeting by the wind or rain driven into the shelters which upsets the birds.

Fertility and hatchability.—Fertility and hatchability, like production, vary with season, being low in autumn and at the beginning of winter. It is again almost impossible to separate the effects of day-length and temperature. Mating activity of cocks is reduced when the temperature is low enough to freeze the combs (LONG and GODFREY, 1952). The fertility of turkey stags can be increased in the early spring by warmth in addition to artificial light (KOSIN, MITCHELL and BURROWS, 1952). Warmth also increases the rate of activation of the testes of starlings (Burger, 1948). Temperatures around 100°F. reduce both the fertility and hatchability of hen's eggs, even when the precaution is taken to store them at the optimal temperature of 55°F. before incubation (Heywang, 1944). In most, but not all, species of mammals the testes have to be kept below the body temperature during the breeding season (*see* Chapter 6). COWLES and NORDSTROM (1946) have suggested, but not yet proved, that the air sacs cool the testes of birds, too, during the breeding season.

EFFECT OF HOT CLIMATES ON EGG SIZE

Residence in a hot climate reduces the egg size of fowls. *Figure 7.36* shows the fall in egg weight of birds kept continuously at a high temperature. In these experiments the shell thickness was affected more than the size, and in earlier experiments the weight of white was reduced more than that of the yolk (Bennion and Warren, 1933). In some recent trials by Warren and his colleagues the effect on shell thickness was not so pronounced (Warren *et al*, 1950). Heywang (1946b) found that he could not prevent the reduction in shell thickness

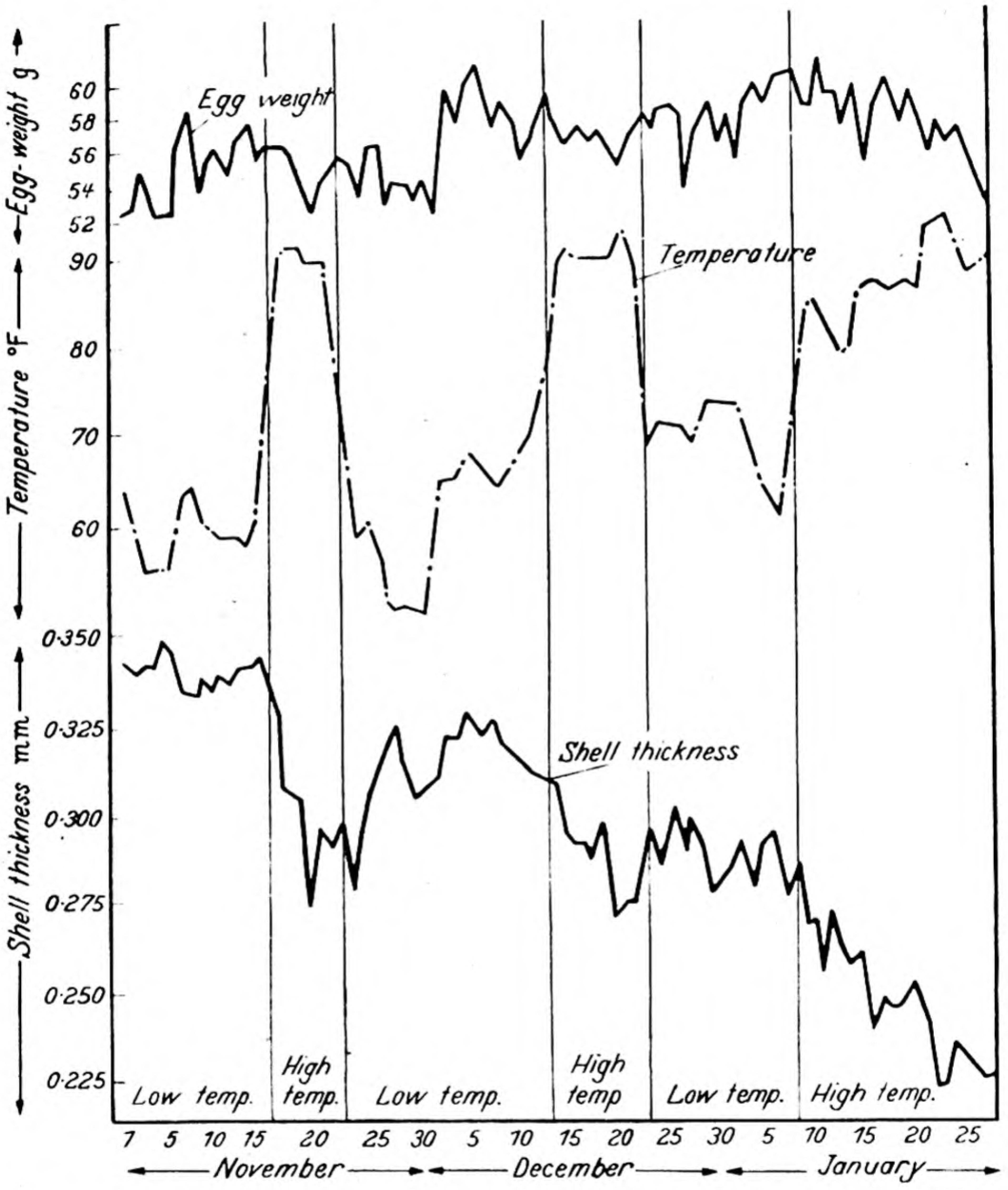

Figure 7.36. The effect of controlled air temperature on shell thickness and egg-weight. High temperature periods 85–93°F.; low temperature periods 55–75°F.; relative humidity 40–60%. The birds were mostly pullets, so the natural curve of egg-weight would have risen rapidly. (From Warren and Schnepel, 1940, by courtesy *Poult. Sci.*)

by using sources of calcium other than $CaCO_3$. Short daily exposures to extreme climates have also been found to reduce egg size considerably (*Figure 7.37*). The duration did not need to be more than 2½ hr. per day. This is rather surprising, because during most of the time over which the eggs were being formed the hens were living in an equable climate. The effects of acclimatization to heat on egg size are not known, but since acclimatization improves heat tolerance, it would be expected to improve egg size. Indeed, ROSENBERG and TANAKA (1951b) have recently suggested on the basis of their egg records that moderately high temperatures, when they are uniform throughout the year, do not seriously affect egg size. On the other hand, Warren and his colleagues found the weight to be slightly less at 65°F. than at lower temperatures.

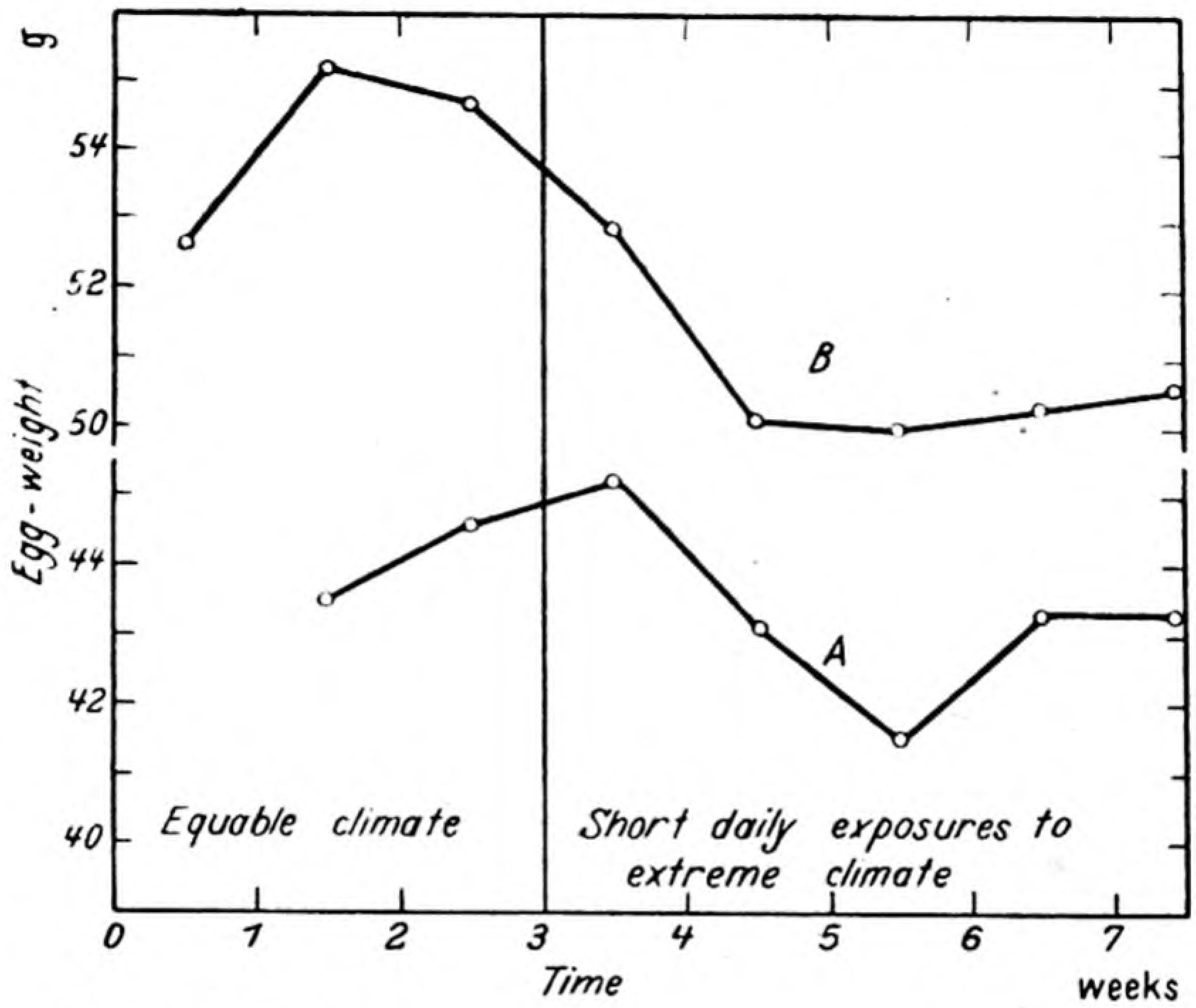

Figure 7.37. Effect of short daily exposures to extreme climates on egg-weight. Dry-bulb temperature of extreme climates 99–104°F., mean radiant temperature within 1°F. of this, humidity 28 mm. Hg vapour pressure and air movement about 20 ft./min. *A*, average for 3 pullets which had just come into lay. The normal curve of egg-size would rise sharply. *B*, average for 3 pullets which had been in production for 2–3 months. (After Hutchinson (1953) by courtesy *Poult. Sci.*)

The effect of high temperatures on egg-shell thickness is of some economic consequence, causing the shells to become fragile in the summer months (Heywang, 1946b). The effect on size, though perhaps not of great economic significance, can lead to confusion when egg records from stock in different localities are compared.

WHY ARE BIRDS RATHER THAN REPTILES USED IN AGRICULTURE ?

The tendency of the poultry industry is to control more and more closely the climate in which fowls live by housing, artificial lighting, etc. If this process is continued, man will end by substituting ectothermic for endothermic heat regulation. This procedure will reduce only slightly the extravagant expenditure of energy to maintain the body temperature above that of the environment (*Figure 7.7*). Thus, the efficiency of conversion of animal into human food is limited, and the performance of even the most improved types of live stock under the best conditions of management is not impressive (*see* Chapters 1, 2 and 3). The fowl, in particular, competes with man for cereal grains, and so it would seem only logical eventually to substitute a poikilotherm, which does not burn large quantities of food to maintain its body temperature. Amongst poikilotherms only reptiles have the appropriate body size to fill the niche occupied by fowls in the human eco-system. When inactive, they are exceedingly economical in energy expenditure (*see* page 339), and the Chelonia, at least, produce eggs and meat which have been prized by man from time immemorial. In Siam the collection of eggs of the baska turtle is a royal prerogative (BOULENGER, 1914). They resemble hen's eggs in size and shape. At one time 48 million eggs of the Amazon terrapin were collected annually for their oil. The giant Gallapagos tortoises, which were much used for meat in the last century, graze and so do not compete with man for cereals.

There are some obvious reasons, irrelevant to this chapter, why the Chelonia are not in general use for agriculture, for example, the long interval between generations, and the low killing out percentage. It is important to know whether there are also reasons connected with heat regulation. Brody (1945) gives some data on the energy conversion of poikilotherms during growth. His conclusion is that, although the metabolic rate is low, poikilotherms grow so slowly that the net conversion is no better than in homeotherms. This is a very important consideration, but Brody quotes data from only two vertebrate species, both fishes. Since efficiency of conversion varies widely in different homeotherms (*cf.* man and pig), it would seem unsafe to assess the performance of poikilotherms from so few species. Moreover, no calculations are given on energy conversion in the reproduction of the larger poikilotherms. A green turtle can lay 200 eggs in a day, and later proceed to lay further clutches, so it is by no means certain that its efficiency is not high.

There are definite reasons why reptiles could not be domesticated over a wide range of climate without control of their environmental temperature. The limits of their distribution are narrower than those of other poikilotherms, and of course of mammals and birds (*Figure 7.38*). These limits are still narrower within species. For example, the slow-worm gets heat stroke far below the 'preferred body temperature' of Bogert's lizards discussed on page 323. The fowl, on the other hand, can live in nearly all climates which are habitable by man, and this is one of its great advantages for use in agriculture. It would be unwise to state dogmatically that reptiles will never be widely domesticated in the future, for terrapins are already farmed on a small scale in North America and tortoises in parts of Africa and Japan (CANSDALE, 1952), and it is possible that their productivity could be greatly improved.

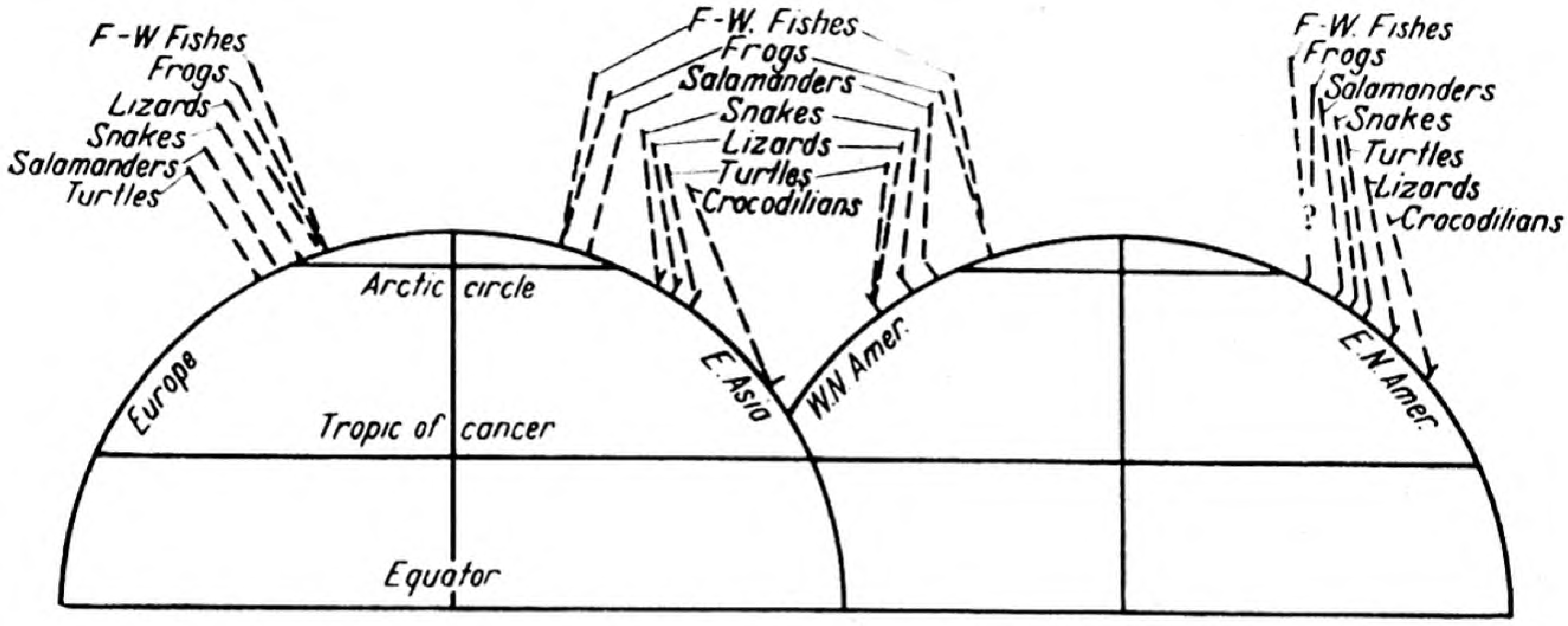
F-W Fishes
Frogs
Lizards
Snakes
Salamanders
Turtles
F-W. Fishes
Frogs
Salamanders
Snakes
Lizards
Turtles
Crocodilians
F-W. Fishes
Frogs
Salamanders
Snakes
Turtles
Lizards
?
Crocodilians
Arctic circle
Tropic of cancer
Equator
Europe
E. Asia
W.N. Amer.
E.N. Amer.

Figure 7.38. Diagram of northern limits of orders of cold-blooded vertebrates. The 2 hemispheres are diagrammatic profiles of the earth from the Equator to the North Pole in the regions named. Points are marked to show the approximate northern limits on the curve of the earth in each region. The diagram is provisional. It is fairly accurate for Europe, next best for western North America, least accurate for eastern Asia and eastern North America. (From Darlington, 1948, by courtesy *Quart. Rev. Biol.*)

The fowl itself is supposed to have been domesticated for cock fighting, not for producing eggs, and to this day the Dinkas of the Sudan make no agricultural use of their birds (LORENZEN, 1948). The adaptation for efficient egg production was the work of man. On the other hand, if in the future homeotherms prove too wasteful in the production of concentrated food for man, there are many other possibilities besides the use of poikilotherms (*e.g.* micro-organisms).

THE PLACE OF CLIMATIC RESEARCH IN THE ADAPTATION OF FOWLS TO UNDEVELOPED AGRICULTURAL AREAS

Most of the improved breeds of live stock were developed in the temperate zone, and naturally the animals were automatically selected to fit the environment. These breeds are often imported into backward areas to improve the local stock, on the ground that this is quicker than selecting from the indigenous animals. It happens that the climate of many of these areas is hot, particularly in the British Colonial

Empire. Exotic breeds often deteriorate in the colonies, and the question arises whether this is because they are ill suited to hot climates, or because they cannot withstand the local diseases and poor nutritional conditions. For this reason there has in recent years been renewed interest in the physiology of heat regulation. For cattle it is already clear that breeds from the temperate zone are not in general well adapted to hot countries, so that the production of heat resisting breeds or strains is a definite requirement. It is true that so far as our present knowledge goes the heat of the sub-tropics and tropics is likely to effect hens more than the cold of temperate climates*; but it is by no means clear that breeds from the temperate zone cannot thrive in hot climates, for in these conditions some flocks give a reasonable egg yield. In the immediate future, therefore, climatic research on poultry is likely to be concerned with the general role of climate in the life of colonial fowls, rather than with the attempt to produce heat tolerant strains or breeds. In particular, the effect of climate needs to be separated from that of nutrition and disease, and for this purpose the laboratory climatic chamber, though in some ways unrealistic, is a convenient tool. It is easy to house a fair number of birds in such rooms, and so to perform experiments on a bigger scale than is possible with the large farm animals, and often the results of such experiments are of general application.

On account of their rapid breeding and the large selection differential which can be applied, fowls are good subjects for the study of genetical adaptation to climate. In fact, as mentioned earlier, it is possible that in the field they become rapidly adapted to exotic conditions in this way. Many other climatic problems in the development of poultry in colonial areas will be obvious from this chapter, so that it is unnecessary to mention them here. But, if climatic research is important, it does not follow that it is all-important in this field of development. The great poultry industry of the temperate zone was the logical outcome of the surplus production of cereals in the early part of this century. Most colonial areas, by contrast, have never been able to grow enough to feed the human population at a reasonable energy level, let alone to provide for poultry, which compete with man for grain. So besides the problems of climate and disease, the repercussions on the human eco-system of an increase or a decrease of poultry need attention. It cannot be said that the human eco-system is self-regulating in such matters, for in the Japanese prison camp at Changi, fowls were kept by the officers at a time when the energy value of the rations was quite inadequate for the human inmates (BRADDON, 1952). Similarly, the keeping of domestic rabbits was advocated in Great Britain during the war of 1939–45, although the agronomical advantages are by no means clear

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* Paradoxically heat stroke has been observed even in the frigid summer climate of Scotland.

(Hutchinson, 1947). It is, therefore, a matter of unusual interest that a Tropical Field Station has recently been established in the Gambia, where such problems may be studied. Here a village is under constant observation, where it is possible to study the net effect of a change in agriculture or other technology upon the health and economy of the inhabitants (PLATT, 1949; MEDICAL RESEARCH COUNCIL, 1952).

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CHAPTER 8

DAYLIGHT CHANGES

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KNOWLEDGE of the important bearing which seasonal change in length of day has on the behaviour and functions of farm livestock has only accumulated to any appreciable extent during the last ten or fifteen years. This is surprising, considering man's intimate association with his animals and his understanding of the various seasonal changes which occur in the natural environment. The explanation probably lies in the fact that heat, cold and the condition of the pastures are more noticeable features of seasonal change than length of day and would therefore tend to be given prior attention.

In 1920, GARNER and ALLARD described the phenomenon of photoperiodism in plants, showing how their reproductive phase may be related to length of day. Then the experiments of ROWAN (1925) showed that the annual rhythm of gonadal development in birds is due not to seasonal changes in temperature, as had been generally believed, but to changes in light. By submitting junco finches to increased illumination with artificial light during the early winter, marked gonadal development was induced and the birds came into song in December (several months before the usual time), despite the fact that they were maintained under conditions of extreme cold.

Experimental enquiries were later extended to mammals. BAKER and RANSON (1932) found that by shortening the daily period of exposure to light from 15 to 9 hours, reproduction in the field mouse almost ceased; then BISSONNETTE (1932a) induced full oestrus in female ferrets some months before the normal time, by subjecting the animals, during winter, to 6 hours' artificial light in addition to the normal daylight hours.

About this time, the illumination of poultry houses in winter, which had been recognized as a practice likely to increase egg production, received more critical attention in the literature. In an important paper WHETHAM (1933) analysed data relating to the response of fowls to light changes and enunciated principles which should now be regarded as fundamental.

These investigations led to further work, still mainly with small species, which confirmed the dependence of the great majority of seasonal breeding animals on light for regulation of their sexual activity. The extensive literature up to this stage has been reviewed by Bissonnette (1936b), Rowan (1938b) and MARSHALL (1942).

Investigations showed that there are considerable species and even breed differences in sensitivity to light changes. Thus while most animals are sexually active in spring, presumably under the influence of lengthening days, there are others which mate in the autumn, probably in response to the decreasing length of days. Marshall (1942) pointed out that there are grades of sensitivity or reactivity between these two extreme cases, there being no month in the year which is not the sexual season of some species of mammal; yet for any particular species (or even breed) the season is extremely regular from year to year.

Attention was focused on farm animals by Marshall's (1937) observation that when sheep are transported across the equator from one hemisphere to another, they finally alter by six months the time of the calendar year at which they breed, so conforming with the seasons in their new environment. This was strong evidence that the seasonal nature of reproduction in sheep must be due largely to some influence of the external environment and Marshall postulated that, if these animals react to light, it must be to diminution and not to increase, as they are autumn breeders.

Experimental evidence that goats (whose reproductive pattern is similar to that of sheep) react to changes in light, and that it is in fact the shortening length of day which is important in inducing sexual activity in their case, was advanced by Bissonnette in 1941. Female goats were given increasing light from January to April and decreasing light from April to July. They were then turned out and mated with males which had been similarly treated, and young were born in December, two months before parturition occurred in the untreated control females.

In the case of sheep, the probable importance of decreasing light continued to be stressed (HAMMOND, 1938a); and HAMMOND, Jun. (1944) observed the incidence of oestrus in a flock of non-pregnant ewes to be evenly spaced about the shortest day. SYKES and COLE (1944) furnished experimental evidence which, although inconclusive, suggested that the sexual season of sheep might be modified by alteration of the light environment. This was fully confirmed by YEATES (1947, 1949) who supplied final proof that light plays the major role in regulating the reproductive pattern of sheep. By adhering to a pre-arranged schedule of lighting in which additional amounts were provided artificially during the winter months (*Figure 8.1*) and decreased amounts (using a blacked-out pen) during the summer, the sexual season of all the experimental ewes was reversed. They came into oestrus in May (when all the control ewes were in anoestrum) and lambed in October (*Figure 8.2*), a time of year quite outside the normal lambing season for Suffolk sheep. The ewes reared the lambs successfully, and this experiment demonstrated not only that oestrus could be induced in sheep by appropriate light treatment, but also that the whole reproductive process including ovulation, gestation, parturition and lactation could proceed.

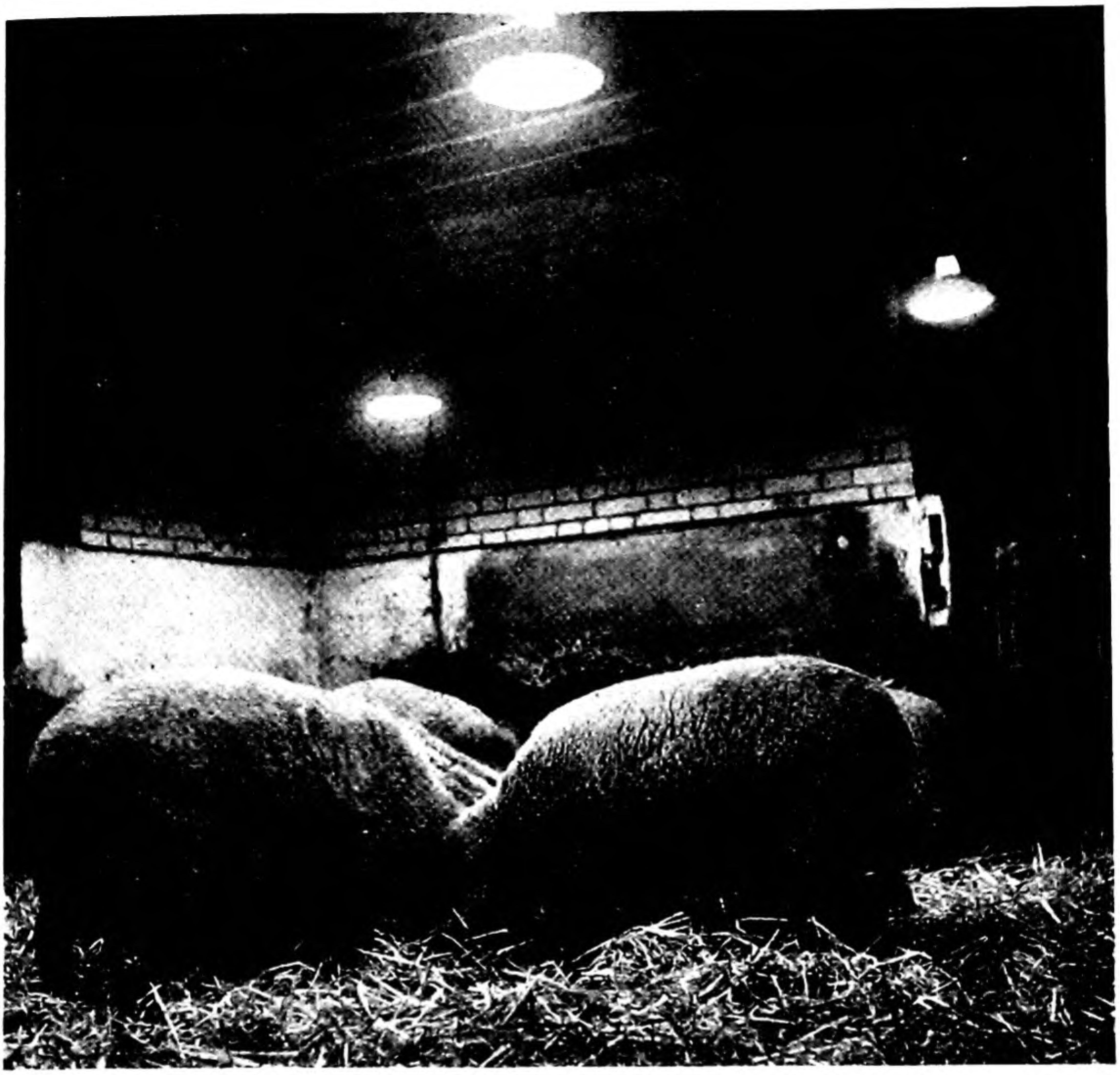

Figure 8.1. Artificial lighting and black-out arrangements for controlling the breeding season of sheep. (Yeates, 1949, by courtesy *J. agric. Sci.*)

That horses are also sensitive to seasonal light changes has been shown by Burkhardt (1947). Mares subjected to additional artificial light during anoestrum in winter were caused to come into oestrus some two months before control animals. In addition, the observation was made that the light treatment hastened the shedding of the winter coat of the experimental mares. This effect of light on the coat has also been observed in cattle by Laing (1948) who subjected cows to additional artificial light in mid-winter.

Although cattle seem, apparently through domestication, almost to have lost their believed original characteristic of seasonality of reproduction, difficulty is experienced, in high latitudes at any rate, in obtaining conceptions in cows during certain months. **Mercier** and **Salisbury** (1947), from a study of three herds of dairy cattle in different latitudes in Canada, found that the lowest percentage of successful services was obtained during winter and spring and the highest during summer and autumn. The average monthly conception rate was significantly correlated with the monthly average length of daylight, there being a lag of approximately 1 to 2 months after the longest day before maximum fertility was reached. Temperature changes had no measurable effect and the authors believe that, at high latitudes, variations in length of daylight significantly influence the fertility level of cattle.

Figure 8.2. Suffolk lambs born in autumn as a result of experimental modification of the mating season of the ewes. (Yeates, 1949, by courtesy *J. agric. Sci.*)

The present position as regards farm livestock, therefore, is that light certainly influences reproduction in poultry, sheep, goats and horses and is probably important in cattle. It is apparently concerned in the coat-shedding of some animals, and there is evidence, which will be discussed later, that it may also affect other functions. Clearly, then, a knowledge of the responses of animals to light is necessary for an understanding of their natural behaviour and for the formulation of any complete system of animal husbandry.

LIGHT EFFECTS

THE BREEDING SEASON AND NATURAL SELECTION

A widespread tendency exists among animals for the birth of young to occur in the spring or early summer, which is a time of year especially favourable for their survival. This necessitates a restricted mating season, ante-dating birth by a period of time equivalent to the duration of pregnancy of the species concerned. As the duration of pregnancy varies widely among species, it is evident that the mating season must vary correspondingly, and this is, in fact, the case.

Among farm animals, for instance, the mare and ewe both tend to produce young in spring : pregnancy lasts for eleven months in the mare and five in the ewe, so that horses mate in spring, and sheep in autumn. Both owe regulation of their sexual function to light change, and the fact that the mare is activated by increasing day-length, whereas a decreasing photoperiod stimulates the ewe, is in no way irreconcilable. There is even evidence that in some species, such as the mink (Hammond, Jun., 1951b), the stimulus is constituted by a mixed pattern of decreasing, followed by increasing, light. Such a response as this latter probably explains those cases in which reproduction commences very soon after the change-over in the seasonal light curve, and in which some phases of the reproductive process (*e.g.* early stages of spermatogenesis) commence before the change-over. The particular way in which species or breeds react to light is unquestionably a genetic characteristic, acquired through natural selection : it simply represents the mechanism by which birth at a particular, favourable time of year, is ensured, and it is quite to be expected that the precise mode of action of the light effect might vary among species or types which, after all, represent different lines of evolutionary descent.

This conception of a genetically controlled reaction to light and its relation to natural selection is well illustrated in sheep. Survey of the breeding behaviour of ewes from widely differing geographical locations shows that there is a gradation in length of the mating season according, in general, to the latitude of their region of origin. Thus sheep indigenous to arctic regions have a very restricted season. The ewes do not come into oestrus until November (Marshall, 1937), so that lambing cannot occur until April, by which time the snow is melting. In these cold regions, the lambs of any ewes which breed too early in the season, *i.e.* those having a genetic make-up predisposing to quick reaction to decreasing light, would be unlikely to survive and pass on this characteristic. Similarly, lambs born late would be unlikely to survive the following winter, and the characteristic of late mating would also be selectively eliminated. In this way, cold-climate breeds have been evolved which, because of their characteristic response to the light environment, mate only during a very restricted portion of the year, corresponding to a time which allows the new-born lambs optimum chance of survival.

In more temperate regions, where temperature and food supply are less likely to be limiting factors to survival, selection has been less restrictive and breeds with a longer sexual season have been established.

Such a theory of natural selection, based on the conception of characteristic response to the light environment, explains both the time of onset and the duration of the sexual season of sheep. Thus HAFEZ (1950) has shown that Scottish Blackfaced, Welsh Mountain and Border Leicester ewes, all ' high latitude ' sheep, have a sexual season which starts late, some 17 weeks after the longest day, and lasts only about 19 weeks ; Romney Marsh and Suffolk sheep, which originated in the milder southern counties of England, breed for an average of 26 weeks; and Dorset Horns, which are believed to owe their origin partly to an infusion of Spanish Merino, have a sexual season which starts early (four weeks after the longest day) and lasts for about 32 weeks. The Merino is well-known to have a still longer sexual season, and this is in keeping with its believed Mediterranean origin.

In tropical and sub-tropical regions, where environmental conditions are more or less constant throughout the year, cold and lack of food have not operated in selection and the fact that sheep indigenous to such regions have the capacity to breed throughout the year (Marshall, 1903 ; SMITH and SINGH, 1938) seems more or less to be expected. In such sheep there has evidently been little or no selection for individuals which might be capable of reacting in any characteristic way to light change. There is little light change in these regions anyway.

A tropical or sub-tropical origin also possibly accounts for the apparent complete unresponsiveness of the pig to seasonal light change. However, the susceptibility of the domestic pig to heat (ROBINSON and LEE, 1941) might suggest that it originated in a temperate, rather than a tropical environment. If that is so, it may be that this species has, by domestication, been ' freed ' from any influence of seasonal change, a process which is apparently still operating in cattle of the European breeds.

IMPLANTATION OF BLASTOCYST

A phenomenon of reproduction which involves seasonal light change, and which further illustrates the complex way in which birth at a suitable time of year is ensured, is that of delayed implantation. PEARSON and ENDERS (1944) showed that the long gestation period in the North American pine marten may be shortened by three months if additional artificial light is provided during the winter. The effect of light is to hasten implantation which would otherwise not occur until the spring. This phenomenon seems to be quite widespread among members of the Mustelidae (Asdell, 1946). In the mink, for instance, embryonic attachment lasts 31 days in a pregnancy which varies from 39 to 76 days, the actual duration of pregnancy apparently depending on whether mating occurs late or early in the spring.

If this effect of light on implantation applies to any farm animals the horse would seem the most likely. For in this species, Hammond (1938b) found in England that mares due to foal early in the season (March) exceeded the average duration of pregnancy by about 20 days and those due to foal late (June) went about 10 days under the average time (*see Figure 8.3*). More recently, Howell and Rollins (1951) have analysed environmental sources of such variation in Arab mares. Season of breeding accounted for 44 per cent of the total variance and level of nutrition for only 5 per cent. This shows that some important environmental influence apart from condition of the pasture is operating to produce the observed seasonal variation, and Howell and Rollins suggest light as a cause. If light is responsible, and this requires investigation, it would seem most likely that, as with such Mustelidae as the mink, it exerts its influence by regulating the time taken for the fertilized ovum to implant.

Month in which due (336 days) to foal.		DURATION OF THE PREGNANCY (DAYS)								
		Average −			Aver-age	Average +				
		11 to 15	6 to 10	1 to 5	336	1 to 5	6 to 10	11 to 15	16 to 20	21 to 25
March	16–31								●	●
April	1–15									
April	16–30							●	●	
May	1–15				●	●	●●			
May	16–31									
June	1–15			●		●				
June	16–30	●	●	●						

Figure 8.3. The variation in the duration of pregnancy in Welsh pony mares due to foal at different times of year. (Hammond, 1938, by courtesy John Arnold.)

The relationship between seasonal light change and time of implantation suggests that, in those species concerned, the uterus requires conditioning in some special way, not yet understood, before implantation may proceed. Hammond, Jun., (1951a) has shown that, in the mink at any rate, implantation is not simply a matter of the supply of progesterone. Accompanying implantation in this species he postulates the presence of an extra-ovarian factor acting upon the uterus, or passing in its secretion to the blastocyst. Certainly it does appear that there must be some such factor, some ' uterotrophic ' hormone, and clearly enough, its production or activity seems to be regulated by light. Further work on this would appear important, for its applications may be wider than already hinted at here. For instance, existence of some special uterotrophic hormone is suggested by, and probably accounts for, the fact that, whereas implantation is satisfactory in ewes whose sexual season has been reversed by light treatment (Yeates, 1949), it is disappointing in those in which ovulation and oestrus have been induced by gonadotrophin injections during the anoestrum (*see* review by ROBINSON, 1951).

COAT SHEDDING AND MOULTING

The characteristic seasonal changes which many animals undergo in respect of their external covering of fur or hair are familiar to all who observe animals in regions outside the tropics. The development, with the approach of winter, of a protective coat and its subsequent shedding in the spring, are functions which assist homeotherms in the maintenance of thermoneutrality and, as such, should be important considerations in animal husbandry: yet surprisingly little is known of either the mechanism or regulation of these functions. Moulting, with subsequent feather growth in birds, is a somewhat similar phenomenon and, as both moulting and coat shedding are apparently influenced by seasonal light change, they will be considered together here. However, it is not intended to imply that the two processes are necessarily analogous.

There is ample evidence that by artificial adjustment of the light environment, the feather changes which occur in many birds can be controlled and that moulting in poultry owes its seasonal occurrence, in part at least, to the light environment (*see*, for instance, ROLLO and DOMM, 1943 ; LARIONOV, 1941). It is also known, however, that things other than light may cause moulting, such, for example, as hypophysectomy (HILL, CORKHILL and PARKES, 1934), the administration of thyroxine (GIACOMINI, 1924) or other thyroactive substances such as iodinated casein (KOSIN and WAKELY, 1948), while a degree of feather loss may also be precipitated by sudden decrease in food supply, fright or sudden exposure to severe heat (LEE *et al*, 1945). There is also, in poultry, some reciprocal relationship between feathering characteristics and egg-production (already shown to be light-influenced). Thus the natural moult in autumn coincides with a period of rest from laying.

In contemplating all these factors which bear on moulting, the importance of two in particular, namely, seasonal light change and the action of thyroxine seems pre-eminent. VAN DER MEULEN (1939) points out that pituitary preparations which are predominantly thyrotrophic cause moulting, whereas those strongly gonadotrophic stimulate ovarian activity. With the knowledge that both moulting and egg production are influenced by light and that the effect of light on egg production is by regulation of gonadotrophic hormone output, the most likely explanation of moulting seems to be that it is precipitated by a particular state of thyroidal activity, seasonally developed through light regulation of the thyrotrophic hormone output of the pituitary. This hypothesis is in accordance with Van der Meulen's belief that fluctuations in secretion of thyrotrophic hormone control the moulting cycle and that these fluctuations are dependent on environmental factors. He mentions light, temperature, or both, as the most important of such environmental factors. However, the fact that the season of moulting may be reversed by artificially reversing the seasonal curve of lighting, in spite of the seasonal temperature curve remaining the same, indicates the importance of light rather than temperature. This is further emphasized by the precise time relationship which always exists between moulting and egg production irrespective of regional variability in temperature. With the availability of radioactive iodine for thyroid research, final identity of the environmental component believed to regulate the apparent seasonal fluctuation of thyroid activity of poultry, should soon be established. The present evidence points to this component being light.

Among the smaller mammals, of which the mink is an example, light has been shown experimentally to regulate the season of moulting as well as reproduction (Hammond, Jun., 1951b) and, according to RITCHIE (1952), reduced daylight is used in the U.S.S.R. to curtail the time needed for fox fur to become prime.

Burkhardt's (1947) demonstration that extra light applied during the winter is effective in causing the shedding of the winter coat of horses, constitutes the main experimental evidence that light is concerned in this role in the case of any of the larger farm animals. However, Laing (1948), in an experiment designed to test the efficacy of light in bringing cows into oestrus with greater regularity in the winter, found that, in these animals, too, shedding of the hair was associated with increased illumination.

Further work is required to confirm and extend these findings for horses and cattle, for the results should have an important bearing on the adaptability of animals transported to a new environment differing markedly in seasonal light characteristics from their original one. It is already known, for instance, that in equatorial regions some cattle of European origin are unable to shed their hair with regularity (*see Figure 8.4*) certain individuals being unable to do so at all (BONSMA, 1943). This disability, which is serious from the point of view of heat regulation, has not yet been satisfactorily explained, but there are good reasons for believing that it may be connected with the tropical light environment, which remains practically uniform throughout the year.

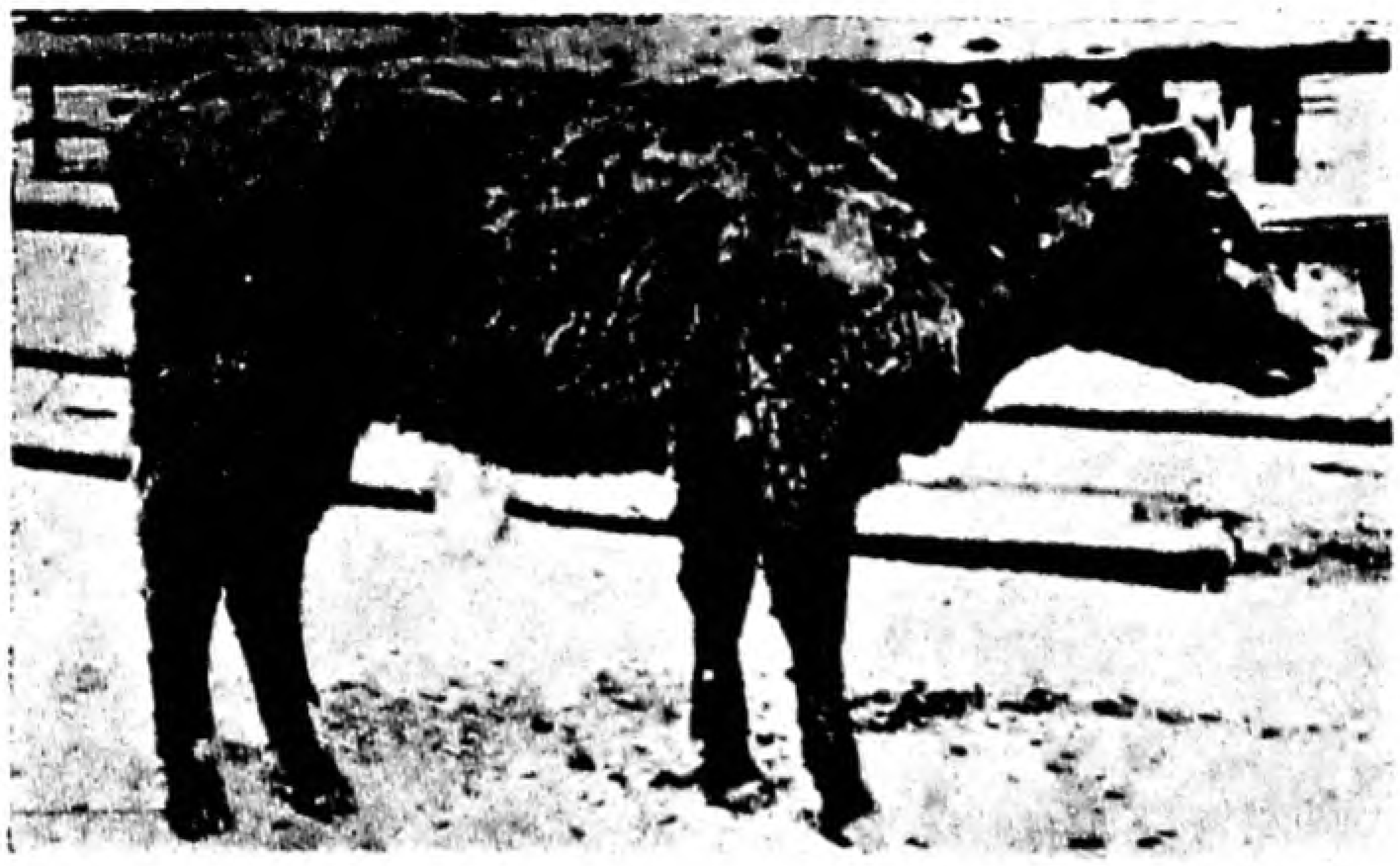

Figure 8.4. This Shorthorn heifer, although 18 months old, had never shed its coat. It received good treatment and was never ill. (Bonsma, 1943). The slowness or failure of some cattle of European origin to shed the long, woolly coat in tropical and sub-tropical regions is little understood, but there is some evidence that the almost constant day-length may be a contributing factor. (By courtesy *Fmg. in S. Afr.*)

It would seem that in trying to evolve suitable strains of European cattle for tropical regions, selection should favour smooth-coated individuals. In sub-tropical regions, either smooth-coated animals or those which shed their coat readily in early summer, *i.e.* those whose coat-shedding mechanism is apparently sensitive to small light changes, should form the breeding stock.

Cattle indigenous to the tropics maintain a smooth, sleek coat throughout the year and are apparently incapable of growing a woolly coat, even if transported to a cold locality or a region of high latitude.

MILK PRODUCTION

The reason for the definite, progressive rise (*see Figure 8.5*) in the milk yield of dairy cattle during the two or three months prior to their being turned out to grass in the spring in England (SANDERS, 1927) has not yet been established. Newer knowledge of the sensitivity of farm livestock to light change allows formulation of the hypothesis (Hammond, 1952) that milk secretion is regulated to some extent by light, through an effect on the lactogenic hormone of the anterior pituitary gland. This hypothesis receives support from **Rako** and **Marinic** (1952) who attributed to light the increased milk yield in a group of cows turned from a barn for several hours each day in spring, into an enclosure in which the light was 20 times as strong as that in the barn.

GROWTH

The possibility that light may exercise some specific effect on growth is suggested by an experiment of **Clegg** and **Sandford** (1951): White Leghorn day-old cockerels exposed to 6-hour periods of alternate light and darkness grew faster than those exposed to 12-hour alternate periods. In another experiment, birds subjected to 2-hour light and darkness periods showed an even greater difference over controls on the 12-hour schedule of change. There was no difference in feed utilization in the various groups.

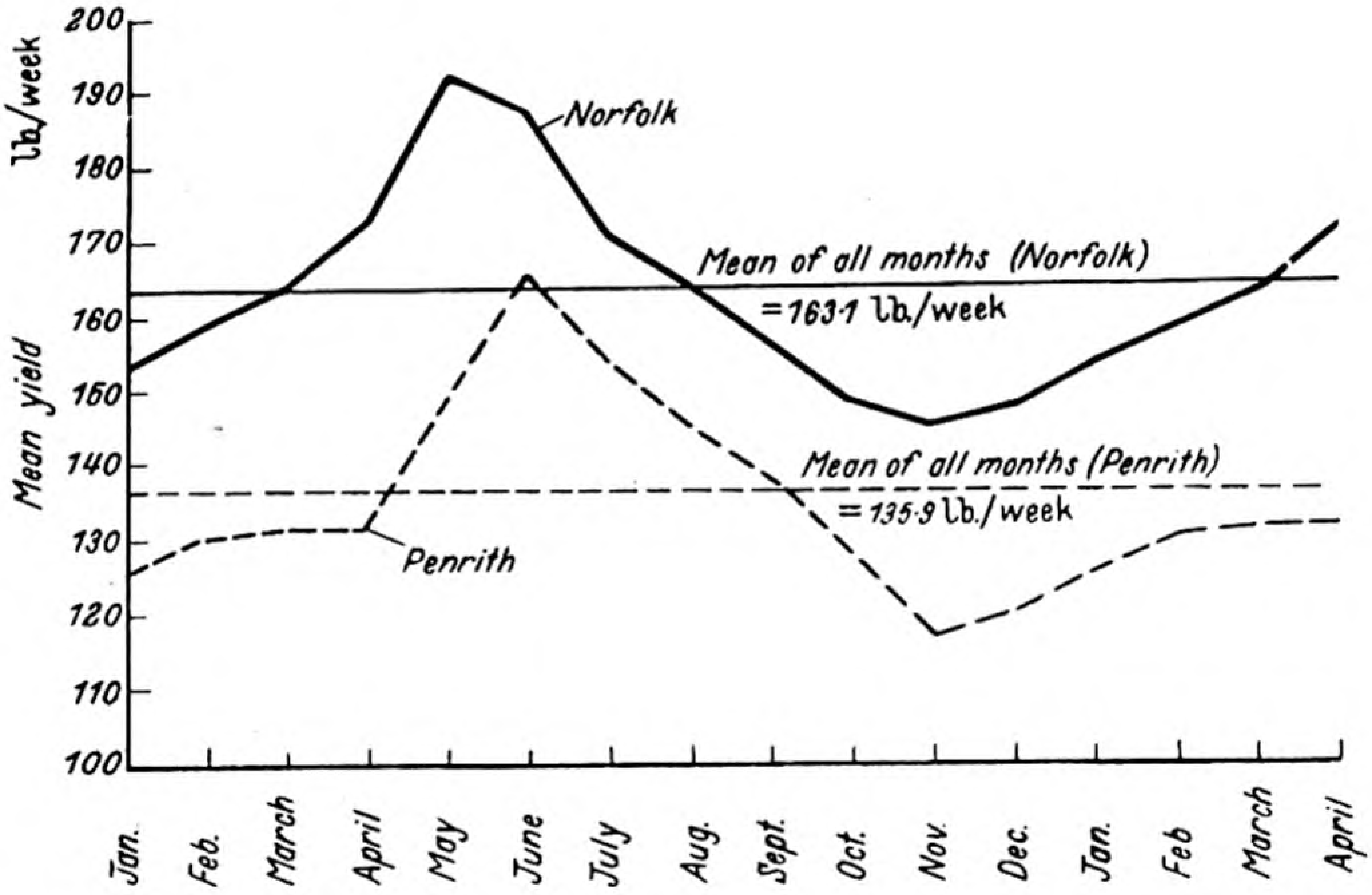

Figure 8.5. Variations in milk yields during different months of the year in two different districts. (Sanders, 1927, by courtesy *J. agric. Sci.*) (The reason for the increasing yields from November to April when feeding is usually constant is not known for certain, but evidence suggests an influence of seasonal light change.)

EXPERIMENTAL LIGHT TREATMENT

INTENSITY AND WAVELENGTH

In some instances only of the large number of experiments in which artificial light has been used to induce sexual activity in birds and mammals, has the relative effectiveness of particular wavelengths and intensities of illumination been investigated. In the majority little attention has been given to these items. The fact that success has so frequently been achieved using a variety of arbitrarily chosen light sources indicates that, within limits, intensity and wavelength are relatively unimportant. This view is supported, at least in the case of intensity, by the fact that ordinary electric lights of from 3 or 4 to about 30 foot-candles, appear to be just as effective as natural sunlight which, on bright days, may have an intensity of several thousand foot-candles. Nevertheless, there must be limits to the intensities and wavelengths which are effective, and these limits may not be the same for all species.

Where lights are to be used commercially in any stock-raising enterprise it is obviously important to keep working costs as low as possible. This necessitates, among other things, a knowledge of the relative effectiveness of various types of lighting.

It appears that in birds, a light intensity of a certain, rather feeble standard is essential for the full photoperiodic response : increase beyond that point has no additive effect (Rowan, 1938b), but below that point the degree of gonadal development varies with the intensity used (Bissonnette, 1931b). For instance, starlings show progressive acceleration in the rate of testicular enlargement and activation when irradiated from the same distance by bulbs of 10W., 15W., and 25W., but with bulbs of 40W. and upwards, the progressive effects cease.

The fact that light intensities above a certain, rather feeble level produce no further response is also borne out by experimental work with poultry. In one trial (NICHOLAS, CALLENBACH and MURPHY, 1944) intensities of illumination varying from 0·5 to 38·0 foot-candles were equally effective in stimulating egg production ; in another (DOBIE, CARVER and ROBERTS, 1946) extra lighting also stimulated production and intensities ranging from 1·0 to 31·3 foot-candles had equal effects.

These findings, based on actual experiments, seem definite enough for birds. In the case of mammals, the lower limit of light intensity necessary to evoke gonadal response has not been investigated. However, there is every indication that, like birds, they are sensitive, photoperiodically, to quite low intensities of illumination, and certainly to those provided by the usual household type of electric light.

Investigations with ferrets have shown that animals placed in cages at distances varying from 1 to 22 feet from a 1,000W. lamp, all have onset of their oestrous cycle hastened (Marshall, 1940). The suggestion that the degree of hastening is roughly related to the intensity of irradiation requires confirming.

Two hours' irradiation each evening from eight lamps of 60W. each is said to be as effective in inducing oestrus in ferrets as a single 60W. lamp used for 16 hours every night (MARSHALL and BOWDEN, 1936). However, since another factor (time) is involved here, full interpretation of the result is difficult. Certainly the experiment shows that one

60W. lamp is sufficient, though not necessarily the minimum intensity requirement, for the photoperiodic gonadal response.

So far as farm animals are concerned minimum intensity requirements for satisfactory control of gonadal function are unknown. In his experiments with goats, Bissonnette (1941) modified the breeding season of the majority of a group of five females, using a single 100W. lamp in a small room. Burkhardt (1947) used a 1,000W. lamp suspended from the roof of a loose-box to accelerate the onset of oestrus in mares. With sheep, Sykes and Cole (1944) used two 100W. bulbs. Yeates (1949) used four 100W. bulbs evenly spaced about a pen measuring 15 ft. × 15 ft., providing an intensity of illumination of about 10 foot-candles at a height of two feet above floor level. HART (1950), in an unusual light treatment of sheep, which will be discussed later, employed two 5 ft., 80W. daylight fluorescent lamps in each pen. These gave an intensity of from 25–30 foot-candles immediately below the lights and of not less than 10 foot-candles elsewhere in the pens, presumably at eye-height of the sheep.

In discussion of the minimum light intensity requirements for full reproductive photoperiodic effect, consideration should be given to the intensity of natural daylight at first morning light and at the last light of day in the evening. The times, in relation to sunrise and sunset, at which effective light intensities ‘ cut in ’ and ‘ cut out ’ respectively, are unknown. Certainly they are different for places separated appreciably in latitude, due to variation in length of twilight ; possibly, too, they are different for various species.

The interval between sunrise and sunset is sometimes selected in photoperiodic experiments as a measure of day-length. This procedure is deprecated, because it takes no account of appreciable light during morning and evening twilight ; also, the duration of twilight varies greatly with latitude. Although it is admittedly an arbitrary choice, a reasonable measure of effective day-length seems to be the time between morning and evening civil twilight. Civil twilight marks the time when ordinary outdoor operations are difficult without artificial light, although there is still ample light to make possible large-scale operations, requiring outline only. It is more accurately defined as the time when the sun has a depression of 6°. Like sunrise and sunset, the times of civil twilight are available from tables of astronomical data, such as the Nautical Almanac. Civil twilight is probably very close to the time at which poultry become active in the morning and go to their perches in the evening, though this has not been investigated. Certainly birds must be very sensitive to changes in intensity at the lower levels for, as Hammond (1952) points out, they go to roost during an eclipse of the sun : also if the artificial lighting provided for poultry in the winter is of insufficient brilliance (as in paraffin lamps of low intensity) it fails to bring the birds off their perches and egg production is not stimulated.

With the knowledge that ordinary white light induces reproductive activity in many birds and mammals, an interesting point arises: is the effect attributable to white light as such or to some particular spectral component or group of components ? A few experimental results on the effectiveness of particular wavelengths are available for ferrets and birds. For ferrets, stimulating radiation extends from the red to the near ultra-violet of the visible spectrum (Marshall and Bowden, 1934, 1936). Red, yellow and green, though each is quite effective, are no more stimulating than white. The heating radiations of long wavelength have very slight or no effect, but ultra-violet causes ferrets to experience oestrus even earlier than when white light is used, and to remain on heat for a longer period after discontinuance of the irradiation.

For birds, too, various colours seem to have nearly equal effect (Rowan, 1938a, b), although at very low intensity red is claimed to be more potent than other colours and green actually inhibitory for promoting testis activity in starlings (Bissonnette, 1932b ; BISSONNETTE and WADLUND, 1931). According to BENOIT, WALTER and ASSENMACHER (1950) testis development was induced in immature male ducks by orange and red lights directed to the orbital region and by indigo, blue and yellow lights directed to the hypothalamus. In each treatment other colours were ineffective. This most astonishing result suggests the rather widespread presence of either receptors or of some light sensitive substance; and in either case, a differential reaction to wavelength according to the locality of interaction. In poultry, birds illuminated for 13 hours each day during the winter months responded equally well when irradiated with white, red or white plus ultra-violet (Dobie, Carver and Roberts, 1946).

For practical requirements, more exact knowledge is required on some of these points relating to intensity and wavelength. In the present state of knowledge the following tentative conclusions seem justifiable : most species have about the same minimum intensity requirement for full effect ; this minimum represents quite a feeble light ; below the minimum, the effect on the gonads dwindles progressively with decreasing light intensity; with the possible exception of ultra-violet (which Marshall and Bowden showed to be especially potent but which, incidentally, is damaging to the eyes), the use of particular wavelengths has no definite advantage over ordinary white light.

TYPE OF APPLICATION

The changes in the duration of daylight to which animals are subjected in the natural environment are gradual and continuous. For six months of the year, in regions outside the tropics, the length of day increases progressively ; for the remaining six months it is decreasing. The amount of this daily change becomes greater the further one moves from the equator, while for any one locality the rate of change is greatest at the equinoctial seasons and least in mid-summer and in mid-winter.

A striking feature of the natural light environment is the regularity with which the yearly changes are repeated in any one latitude. The annual light cycles for a particular locality are virtually identical, a condition which is far from being the case with other environmental factors such as temperature, humidity, wind, rainfall or pasturage. It is not perhaps surprising, therefore, that in the course of evolution, light change is the environmental factor by which animals have adapted themselves to seasonal effects as a whole, as, for instance, in ensuring the birth of young at a suitable season.

It will later be shown that the light, generally perceived by the eye registers its effect through the anterior pituitary gland. But because, through natural selection, the retino-pituitary mechanism of light-sensitive animals has developed in, and now reacts to, the particular light environment encountered naturally, it does not necessarily follow that other types of light treatment might not also be effective stimulators. As already mentioned, for instance, light sources differing greatly from sunlight in both wavelength and intensity may effectively evoke the light-gonadal response. But what of the duration of lighting ? Need the changes be gradual and continuous, as in Nature ? Obviously knowledge on this point is desirable if artificial light environments are to be used either experimentally or commercially, in live-stock raising. The question cannot be answered fully yet, for, unfortunately, although a great many different light treatments have been tried, few experiments give precise details of effects on both sexes or state whether sexual activity was followed by normal pregnancy. Nevertheless a considerable amount of useful information is available.

In his original experiments with ferrets, Bissonnette (1932a) subjected males and females to a sudden large increase in light in the autumn, the light being turned on for six hours each night after nightfall. This treatment was effective for females (as far as can be judged without the complete proof of normal gestation, parturition and lactation), but was not completely effective for males, since spermatogenesis did not proceed beyond the secondary spermatocyte stage. In later investigations, Bissonnette (1935a) subjected ferrets to gradual light increases and this treatment was found to be effective for both sexes. Females were brought into oestrus and kept in that condition for a long while by increasing the light steadily up to 18 hours per day. But when the light was gradually reduced to 16 hours they went into anoestrum just as readily as when the light was experimentally reduced to eight hours. These findings suggest the desirability of gradual and continuous light changes as against a sudden, large, fixed change, and they show that, as with sheep (Yeates, 1949), gonadal response in the ferret is unrelated to specific threshold levels of lighting.

Among birds, Rowan (1938b) believes that in junco finches complete normality of gonadal development depends on slight, progressive advances in the length of illumination, longer jumps affecting the birds adversely. The probable importance of small additional increments has also been stressed by Whetham (1933) who believes that the stimulus responsible for increased egg production in poultry is provided by the differences in the light ration and not by any particular amount of light. She points out that when birds are maintained on a constant amount of light, even though the level is a high one, the effect wears off, whereas high production is maintained if the light ration is continually increasing.

There is no doubt that in poultry (and also in many of the spring and summer mating species of birds and mammals) a sudden change to a high level of light in the autumn or winter produces a quick response. Much of the experimental work has not been continued beyond the stage of the initial response and a belief, which is not satisfactorily substantiated, tends to exist, that activity is due simply to a high level of lighting. Furthermore, types of light treatment other than gradual changes frequently result in the gonads of birds developing from the small, quiescent state, at a faster rate than they do under natural conditions. Whether or not such rapid responses are compatible with full reproductive function requires more investigation.

In a long-term experiment with sheep (Yeates, 1949), the breeding season of ewes was successfully reversed by using gradual changes. Alterations to the daily amount of light were made each week, thus approximating fairly closely the slow but continuous changes which occur naturally (*see Figure 8.6*). This treatment was effective for both males and females: the ewes lambed out of season and, in the rams, the decline in libido and semen quality, which normally occurs in the spring and summer, was replaced by a period of high fertility. The ewes came into oestrus after approximately the same interval on a decreasing plane of light as they do under natural conditions and, in general, the results provided information on the way sheep react under natural conditions.

Recently ferrets have been brought into oestrus by the unusual treatment of subjecting them to an additional hour of light in the middle of each night (Hart, 1951), a method which was found effective in photo-periodic investigations with certain plants (BORTHWICK, 1947). There can be no doubt that the onset of reproductive activity was greatly hastened in the experimental female ferrets, and the rapidity with which the response was elicited indicates that this method of stimulation may be particularly potent. No details of spermatogenesis under this type of treatment are available but apparently litters have resulted from matings of treated males and females. The pronounced hastening of the onset of oestrus by this method suggests that one way in which the pituitary may be activated is through a contrast-sensitive mechanism which is stimulated by light-dark sequences. This suggestion is supported by experimental evidence with birds, KIRKPATRICK and LEOPOLD (1952) having demonstrated that a daily quota of 10 hours of light including a one-hour light interruption of the night causes development of the reproductive organs of the bobwhite quail, whereas the same light ration, applied as a single daily exposure, fails to cause development. Reproduction in the bobwhite quail is brought on by long days and, as this is also the case with poultry, the latter are probably also sensitive to light interruption of the night. Even if this is so, however, some demonstration that the initial stimulus is maintained by continuance of treatment will be necessary before it could be recommended for practical use. Such information is unavailable for the quail as the birds were sacrificed only 37 days after the start of treatment, in order that examination of reproductive organs might be made.

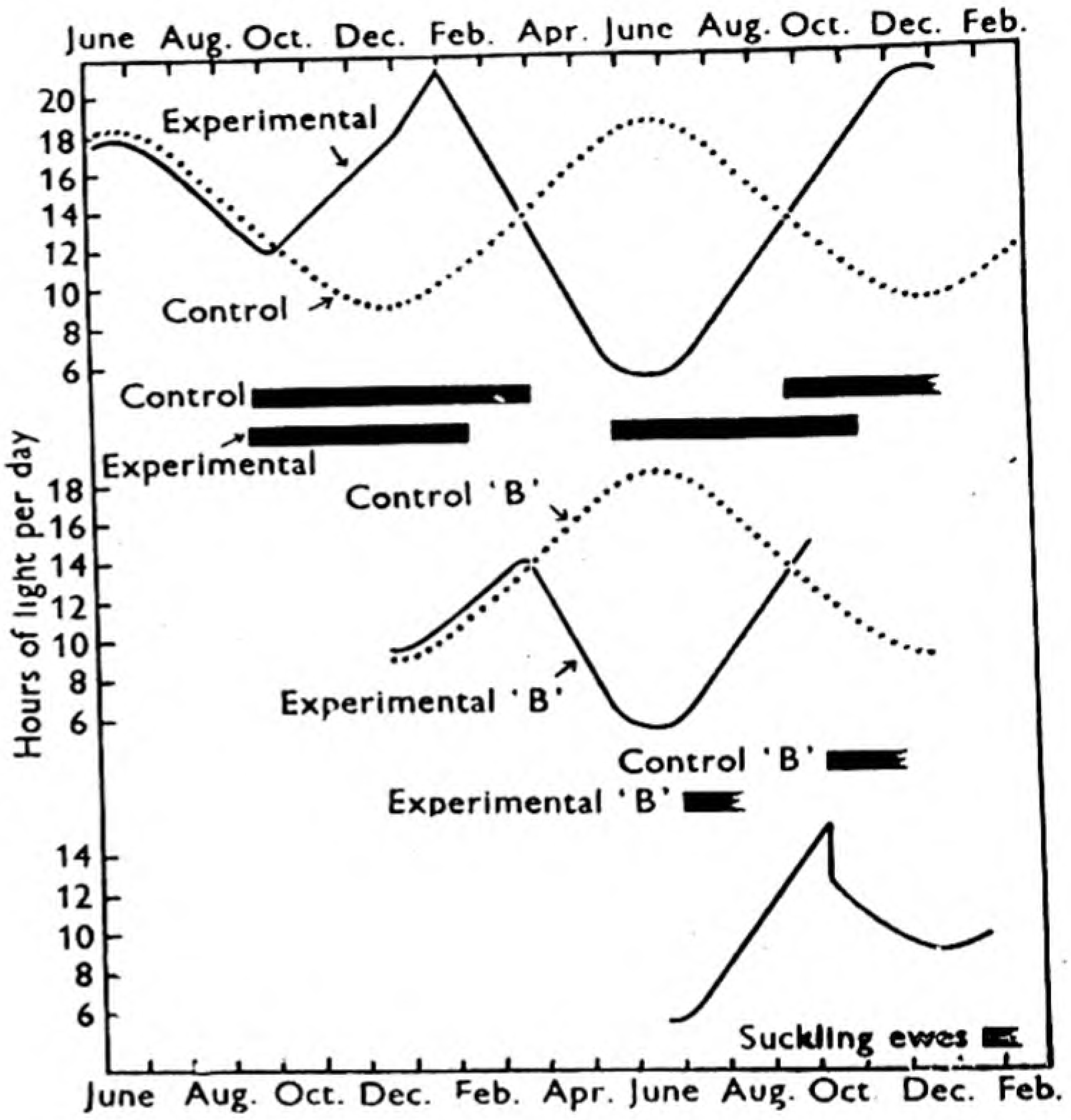

Figure 8.6. Diagram showing the sexual season of several groups of Suffolk ewes subjected to different lighting conditions. The sexual season in each case is shown as a black band beneath the corresponding light curve. In all cases oestrus started 10–14 weeks after the change-over from increasing to decreasing light. (Yeates, 1949, by courtesy *J. agric. Sci.*)

Applying the principle of light-dark contrast sequences to sheep, Hart (1950) has stimulated oestrus out of season by providing a sequence of 4 hours light, 2 hours dark, 4 hours light, 14 hours dark, every 24-hour period. This treatment induced oestrus in the short average time of 30 days, the range being from 8 to 50 days for 10 ewes.

In spite of many matings pregnancy did not ensue. Oestrus cycles, though somewhat sporadic, conformed reasonably well to the normal 16½-day interval and failure to conceive was probably due to infertility of the rams each of which apparently received a mixture of three different light treatments. If further work establishes that the method promotes full spermatogenesis in rams, and results in normal conceptions and lambings, it will be an important advance for, in principle, it represents a practical and cheap method for use on a commercial scale. All it really entails is utilizing the normal summer day as the light source and running the ewes into a blacked-out shed or pen for an hour or two of total darkness in the middle of the day. The theoretical explanation of the method's effectiveness is that sheep, being ' short-day breeding ' animals, are simulated by a light-dark contrast sequence in which the dark period is lengthy compared with the light. It is argued that a period of about two hours' darkness in the middle of the spring-summer day is sufficient to divide the long light period into two short light periods, which then contrast sufficiently on either side of the long dark period of night to establish the activating rhythm.

Striking results were obtained in ducks by Benoit (1936) who subjected the birds to light for 10½ minutes every hour during 14 hours of the night for 16 days. He contends that for a light of given spectral components, the intensity and duration of its action are not the only factors which influence the response, but that the progressive augmentation of applications and the fractionation of those applications are important. Whether or not the principle of fractionation of applications applies under natural conditions, is difficult to say. It may be that the changes from light to darkness and *vice versa* every 24 hours provide a particular stimulus and that by increasing the frequency of these changes by artificial means, a stimulus which already operates in some limited way under natural conditions is being applied more intensively. On the other hand, artificial fractionation of the light (or darkness) periods may have no connexion with any natural events and may be effective in producing such rapid gonadal response, purely by chance. In the latter case there then seems no reason why other types of light stimuli, also effective, but unrelated to the natural environment, may not be discovered. Indeed, the so-called ' light shock ' effect in poultry (Staffe, 1950) by which production was increased through flashing on a 1,500W. lamp occasionally for 20 seconds during the night possibly falls into this category.

MECHANISM OF LIGHT ACTION

The mechanism by which the gonads may be influenced by environmental light changes has been studied mainly in birds and small animals. A good deal of information has accumulated and, for the species studied, a broad outline of the physiology involved has, by degrees, been pieced together. This, perhaps too generously, tends to be extended to include all species in which reproduction is influenced by light changes.

The anterior pituitary gland, well known to exercise control over the development and activity of the gonads, is now generally recognized as playing a dominant role in the light-gonadal response (Marshall, 1936, 1937 ; Rowan, 1938b). It is accepted as being the organ primarily affected, activation of the gonads following secondarily as a result of some light-induced pituitary change. Such intermediation of the pituitary is supported (though not proved) by the fact that hypophysectomized female ferrets are incapable of reacting to the light stimulus (HILL and PARKES, 1933).

Although it is agreed that the pituitary is the regulator, there is some uncertainty as to the exact manner in which the light environment exercises its effect on this organ. The most widely held view is that the eye acts as a light receptor and, presumably by the transmission of impulses from it along neural pathways, the pituitary is stimulated. This view is strengthened by the recent finding of THOMSON (1951) that the gonadal response to light in ferrets depends on the integrity of the ganglion cell layer of the retina and by his conclusion that the initial mechanism in the transference of light stimuli from the eye to the hypophysis is a nervous one.

In conceding the participation of the central nervous system, some investigators (*e.g.* PARKER *et al*, 1952) emphasize the presence in nervous tissue of characteristic porphyrins. These porphyrins, it is suggested, might be concerned (by virtue of their believed photochemical reactivity to particular radiations) with light-activation of the pituitary. Such an hypothesis, which at present amounts only to speculation, might account for the apparent effectiveness of light shone directly on to the hypothalamus, as described by Benoit, Walter and Assenmacher (1950), and mentioned previously.

Bissonnette (1936a, b) found that when the heads of ferrets were covered with hoods the animals were unresponsive to additional lighting in the winter, but when holes were cut to expose the eyes, the lighting was effective. He also found that severing the optic nerve made the sexual cycle independent of any seasonal influence. From observations on sparrows, RINGOEN and KRISCHBAUM (1939) also concluded that there was no gonadal response to light if the eyes were covered. Burkhardt (1947) observed that mares, if hooded, were unresponsive to additional lighting in winter. Blind ferrets (Marshall and Bowden, 1934) and blind white-footed mice (WHITAKER, 1940) apparently do not exhibit any cyclic tendency to breeding activity.

Benoit, whose many investigations on ducks have been critically examined by Rowan (1938b), advances evidence that the eye itself is not necessarily involved. Ducks draped entirely in light-proof cloth failed to respond to light while those with perforations left for exposure of the eyes did react. Extirpation of the eyes and severance of the optic nerve did not, however, prevent gonadal stimulation following increased illumination, from which it appears that receptors might be located near the eyes without the eyes necessarily being themselves involved. However, as a result of subsequent investigation, Benoit claims that in ducks, complete removal of the eye or destruction of the optic nerve does not affect the issue, as he believes that the administered light is capable of penetrating the tissues of the head and bones of the skull and so reaching the hypophysis (or some region close to it), without passing through the eye. There is no evidence among mammals that light can have any effect through penetrating the skull in this way, and indeed it seems most unlikely in view of the greater thickness of the skull in mammals.

On the assumption that the eye is the receptor in mammals, attempts have been made to define neural pathways by which impulses might be transmitted from the eye to the anterior pituitary (CLARK, McKEOWN and ZUCKERMAN, 1938 ; COLLIN, 1938). These suggest that possible pathways exist, along which retinal impulses could be relayed to the hypothalamus ; but the nervous connexions between the hypothalamus and anterior pituitary are so scanty that neural transmission in this region must be considered extremely unlikely (RASMUSSEN, 1938).

There is no doubt that a close physiological relationship exists between the hypothalamus and the anterior pituitary (HARRIS, 1937; DEY, 1941) and the suggestion of Harris (1949) that the link between the two may be through the hypophysial portal vessels, is based on substantial evidence. Although the nerve supply to the adenohypophysis is meagre, the vascular link (in the form of the portal vessels), between the median eminence and the adenohypophysis, is well developed, and Harris considers it probable that the nervous system regulates the activity of the adenohypophysis by means of a humoral relay through these vessels. The observations of GREEN and HARRIS (1949) on the direction of flow in hypophysial portal vessels of the living rat substantiate this view, and the combined cholinergic and adrenergic nature of such a link, at any rate as far as ovulation in the rat and rabbit is concerned, has been postulated by MARKEE, EVERETT and SAWYER (1952). These latter workers consider that a specific ' sex centre ', located in the hypothalamus, activates the pituitary through the above-mentioned link.

It has been pointed out by ZUCKERMAN (1947) that there are apparently no recorded experiments on the effect of light changes on animals in which the pituitary has been removed from its normal site and successfully grafted on to some other tissue in the same animal. If this could be done with a sure knowledge that removal of the pituitary had been complete and that the graft was functional, it should establish whether or not nervous connexions to the pituitary are necessary for induction of the light responses. Recently, however, Jacobsohn and Harris (cited by Markee, Everett and Sawyer, 1952) have found that pituitary transplants in the rat sella become functionally competent to maintain oestrus cycles, whereas transplants under the temporal lobe of the brain (outside the range of the portal system) do not. These findings indicate that, for cyclic activity in the rat, integrity of nervous connexions is unimportant but that close association of the pituitary with the hypophysial portal system is entirely necessary, other vascular connexions apparently being unsatisfactory as substitutes. Whether or not these findings relating to oestrus in the rat apply equally to regulation, by light, of the mating season of seasonal breeding species remains to be found.

The foregoing discussion has been based on the assumption that light, received by the eye (or possibly some region close to it), regulates the seasonal activity of the pituitary of those animals sensitive to light change. A second hypothesis put forward by Rowan (1928, 1938a, b) is that light is concerned only in so far as it provides a means of keeping the animals awake, and that stimulation of the pituitary is effected by changes in metabolism induced by lengthening the period of diurnal activity. Rowan states that gonadal development has been induced in birds submitted to enforced wakefulness in light below the intensity required to induce sexual development. He has further suggested that failure of hooded or blinded animals to respond to light is simply due to their not maintaining wakefulness over the allotted period of time. He states that if such blinded animals are kept in the same enclosure as unblinded individuals, the gonads of all develop at the same rate and this, he suggests, is because the blinded animals have wakefulness enforced on them by the unblinded.

A good many authors (Marshall and Bowden, 1934; Bissonnette, 1936a; Burkhardt, 1947; and others) have put forward the view that the onset of sexual activity cannot be due simply to increased physical exercise and movement. Benoit (1935) has shown that birds trussed so that free movement was impossible, reacted just as quickly to increased lighting as did birds receiving similar light but permitted complete freedom. However, Rowan (1938b) contends that although muscular activity might be reduced to a minimum, it does not affect the argument that wakefulness, rather than light as such, might be the important factor.

The theory that a certain degree or state of consciousness might evoke stimulation of the pituitary seems possible, but the experimental evidence in support of the theory is meagre, and parts of it are open to criticism. Furthermore, experiments by Bissonnette (1931a, 1933) with starlings showed that although added light periods during the winter months induced gonadal activity, added work periods without additional light were not effective. RILEY (1940) also states that in male house sparrows, additional light caused marked enlargement of the testes, but forced exercise on a rotating drum in complete darkness had no effect.

It has sometimes been suggested (particularly in the case of poultry) that the changes induced by increased lighting are due to the longer day available for feeding (Fairbanks and Rice, 1924). However, Hammond (1934), who believes the effect in poultry to be due to stimulation of the pituitary gland rather than to the longer day for feeding, points out that the effect of a continuous 12-hour light soon wears off, whereas a lower but increasing light ration continues to stimulate production. CALLENBACH, NICHOLAS and MURPHY (1943) who investigated experimentally the effect of light and availability of feed on egg production, state that increased exposure to light resulted in superior production during the months of short days, but availability of feed had no observable influence. In light experiments which have been reported with farm animals, the quantity of feed supplied to control and experimental animals has generally been stated to be the same, so, in these cases at any rate, food supply could have had no bearing on the observed differences in reproductive activity.

There is a possibility that seasonal breeding animals possess an internal or ' inherent ' rhythm of sexual periodicity, quite apart from any capacity they may have to respond to external factors such as light. However, although recent opinion (BULLOUGH, 1951) tends to regard its existence as certain, the evidence on which this is based is not altogether satisfactory.

From time to time the idea of an internal rhythm has been postulated to account for apparent anomalies in breeding behaviour. For instance Marshall (1936, 1937) and DUKE OF BEDFORD and MARSHALL (1942) used it to account for ' antagonistic ' tendencies in the reproductive performance of some animals when first transferred to a new latitude. Its presence was also suggested by the eventual spontaneous regression of the gonads of male ferrets (Bissonnette, 1935b) and ducks (Benoit, 1938), when light treatment was prolonged, though in the latter case, other possibilities such as failure or refractoriness of the pituitary gland were recognized as possibilities. Similarly, there is the case of certain spring breeders which become quiescent sexually before the days stop lengthening in mid-summer ; or that (quoted by Bullough, 1951) of the golden crowned sparrow in which the gonads are ' resistant ' to the stimulus of an experimentally increasing day-length until after the month of November (in the northern hemisphere). Bullough also makes special mention of experiments with ferrets in which the imposition of almost continual darkness at a time when the days have only just commenced to lengthen (the experiment was started 24th January) does not infallibly prevent the maturation of the gonads, and also those with minnows in which the same type of treatment does no more than delay gonad growth.

In the light of recent research these seemingly anomalous cases (best considered in two different categories) are now capable of straightforward explanation without the necessity for postulating the existence of an internal or ‘ inherent ’ rhythm. In the first category falls the case of animals transported to the opposite hemisphere. Although it is no doubt true that for a time there may be two ‘ antagonistic ’ tendencies, both of them result from the influence of the light environment, one stimulus or influence having been received in the old environment and requiring a particular time (depending on the species or breed) to die out, and the other in the new. The precise details of breeding following transference depend on the time of year of the movement and on the reaction time to light of the individual animal concerned. These details (for some of which *see* 388) have been worked out for sheep (Yeates, 1949), and the same principle undoubtedly applies for the horse.

The other examples cited as having been used to argue the existence of an internal rhythm come into a second category in which there has been, in the past, an unwarranted assumption that the animals concerned, because they are spring breeders, are stimulated entirely by increasing light. The fact is, as previously mentioned, that early spring breeders may owe stimulation to a mixed pattern of decreasing, followed by increasing day-length. Before it can be stated categorically that anomalous breeding behaviour or even failure to breed under some arbitrarily selected lighting schedule denotes the intervention of an internal factor, there must be a greater appreciation of what constitutes the correct, or at any rate a satisfactory, stimulus. Further investigation in this very open field of work is required to supply such additional knowledge.

Contra evidence for the existence, in sheep, of any inherent rhythm of reproductive activity is provided by experiments (Yeates, 1949) in which various groups of ewes were brought into oestrus by suitable light treatment at different times of the year with equal ease, *i.e.* after approximately the same time-interval following change-over from increasing to decreasing daily light exposure. It is argued from this that no inherent rhythm exists, for if it did, the difficulty or delay with which activity could be induced would vary from time to time according to whether the internal effect was being assisted or opposed. This same reasoning may also be used to argue the non-participation of seasonal effects other than light in the induction of seasonal reproductive activity in sheep.

Summarizing, it appears that the most widely supported and likely mechanism of pituitary regulation by light is that involving the eye as receptor, with neural transmission of impulses or stimuli to the vicinity of the hypothalamus, transmission to the pituitary being completed by a humoral relay involving the hypophysial portal blood vessels. Evidence that light has a direct effect on the pituitary without intermediation of the eye or that its effect is due to wakefulness or opportunity for increased food intake is either unconfirmed or unsatisfactory. The belief that light-responsive seasonal breeding animals possess an ‘ inherent ’ rhythm of sexual periodicity which determines in part the season of year at which they mate, is not supported by recent findings.

PRACTICAL CONSIDERATIONS

LIGHTING OF POULTRY HOUSES

The stimulation of egg production by artificially illuminating poultry houses at night during the winter months, is a practice which is quite well-known and widely employed, particularly in countries of high latitude where the winter nights are long. Ordinary household-type electric bulbs are used and time switches are available for incorporation in the electric circuit. These switches will turn the lights on or off at any desired, pre-set time, so there is no additional labour required to operate the scheme. Unquestionably, production is stimulated and, as prices are generally high in the winter months, there is good return for the eggs produced.

A point on which confusion seems to exist, however, is the exact type of lighting programme to adopt. One popular method is to commence treatment in the autumn, switching the lights on at four o’clock every morning until lighting is finally discontinued in the spring. Another practice is to adjust the artificial supplements to the natural daylight in such a way that the birds receive a constant amount of light—generally 14 hours per day. This latter practice apparently arises from a belief that some threshold level of lighting is necessary and that, of the various levels which might be used, 14 hours per day represents the ‘ optimum ’. However, although an increase to 14 hours per day from some lower level will stimulate production initially, the effect gradually wears off. Further use of the same level of lighting then causes both moulting and egg-laying to assume more or less continuous phases of lessened activity (Larionov, 1941), such as would be expected of similar birds in a tropical light environment.

The type of light curve obtained by turning on the lights at 4 o’clock every morning during the months of short days is illustrated by curve *B* in *Figure 8.7*. This shows the fallacy of such a procedure, for although with the first flush of treatment there is a sudden jump in the level of lighting, which stimulates production, the day-to-day level actually falls again from then until the shortest day, so probably acting, if anything, as a depressant.

Available evidence indicates that, however high the level of light, the stimulus is provided and maintained by the continuous application of increments. On this basis, the lighting schedule likely to achieve best results would seem to be one in which the daily photoperiod is caused to increase continuously, right from the time of the longest day. This is illustrated by curve *C* in *Figure 8.7*. Such a scheme of lighting following the normal summer laying period should suppress the autumn moult and maintain the birds in production until mid-winter, after which they could be disposed of. Alternatively, if a short rest period for the birds is desired, a scheme of lighting such as that represented by curve *D* in *Figure 8.7* could be implemented. This should enable the autumn moult to take place (under the influence of the naturally decreasing light) and then, by virtue of the artificially imposed increments, activate egg-production some two to three months before the normal time.

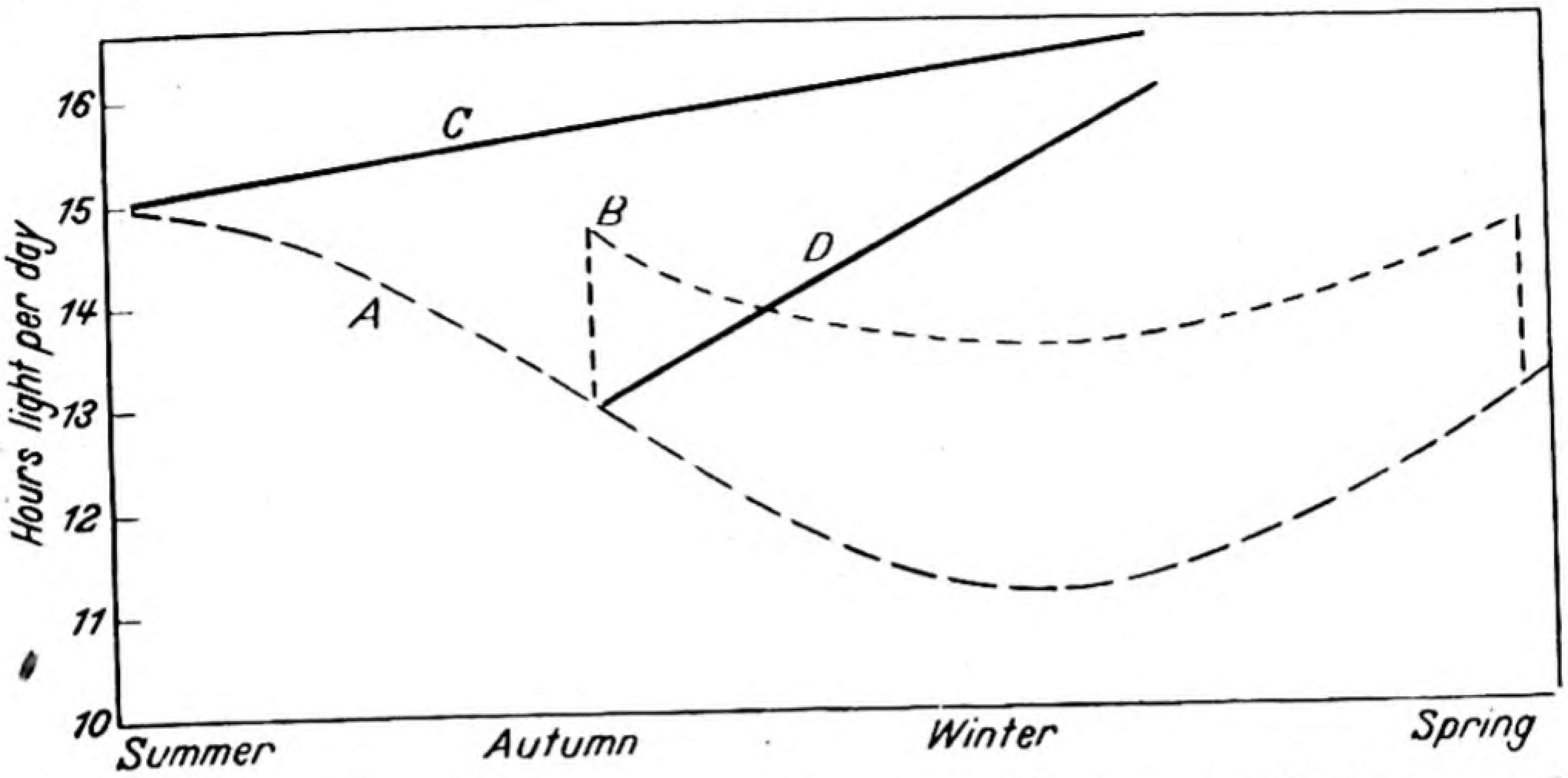

Figure 8.7. Showing (curve A) seasonal change in hours of daylight per day at lat. 28½° (*e.g.* Brisbane or Delhi) ; B, light experienced by poultry at that latitude if artificial lights are switched on at 4 a.m. each day during the "short-day" months. C and D represent curves of lighting either of which should, theoretically, be preferable to B for increased egg production during the months of decreasing daylight.

A point to be appreciated is that, whatever type of lighting programme is adopted, any sudden cessation of the treatment in the spring, will, if such curtailment involves a drop in the daily photoperiod, tend to throw birds out of production. In practice, probably the best way of overcoming this difficulty is to use light treatment only on birds coming due for culling and to dispose of them at the conclusion of the lighting programme.

OUT-OF-SEASON SHEEP BREEDING

Owing mainly to the unreliability of hormone injection methods, artificial alteration of the light environment represents the surest way, at present, of achieving out-of-season lambing in those breeds of sheep having seasonal reproduction. But unfortunately the possibilities of using the light change method commercially are limited by the necessity for housing the sheep, a procedure which, under extensive farming conditions, presents practical difficulty. However, in certain countries such as Canada and parts of U.S.A., where sheep are often housed in any case because of the cold, suitable buildings are available and it would seem quite feasible, if warranted on economic grounds, to use the method to arrange lambings for the most desired time of year.

Certainly the method can be an aid in research, not only by providing suitably conditioned animals for breeding all the year round and so hastening results, but also in the investigation of possible effects of other environmental variables which are normally inseparable from light. For example, observation of the low birth-weight of lambs following a summer gestation (made possible by light treatment) has led to the recent finding (Yeates, 1953) that high environmental temperature, though having no effect on the incidence of oestrus, may be inimical to satisfactory gestation in the ewe.

TRANSFER OF STOCK TO A NEW ENVIRONMENT

If seasonal breeding animals which are responsive to light change are transported to a locality having an appreciably different length of day, their normal rhythm of reproductive activity will be disturbed. Clearly, a knowledge of the nature and extent of the particular disturbance likely to be involved is desirable, for it will allow planning of the movement for the most opportune time of year, or alternatively, the adoption of some corrective or compensating measures. And fortunately, as a direct result of recent experimentation, there is now reasonably good knowledge of these matters, though the effects of the tropical light environment are still little understood.

The most obvious and complete light-season reversal is that experienced by an animal moved suddenly from the northern to the southern hemisphere, or *vice versa*, especially when the two locations concerned are of high latitude. Many instances of the breeding behaviour of animals, particularly British breeds of sheep, moved in this way have been reported (Marshall, 1937), sometimes with apparently conflicting results in subsequent reproductive performance. Thus sheep sent from the British Isles to South Africa and South America have sometimes been reported as having two lamb crops the first year, whereas other consignments remained barren for a whole year or more, all ewes, however, eventually settling down to the annual breeding time typical of the new environment.

Analysed in terms of the time of year of the transfer and the known reaction time to light changes of the animals concerned, these apparently irreconcilable reports have been satisfactorily explained (Yeates, 1949). Furthermore, on the basis of an understanding of these points, the most opportune time for a breeder in the southern hemisphere to import ewes from Great Britain or other northern hemisphere countries may be suggested. Owing to the completely reversed light environment to which the transported ewes are subjected, they will either have opportunity for two pregnancies within a year, or remain in anoestrum for an unusually long time, depending on the time of year of the shipment. One suitable plan would be to purchase pregnant ewes, shipping them as soon as possible after the northern autumnal equinox, say as soon as conception could be reasonably assured in October. In this way the ewes would not be subjected to any sudden, large change in the daily level of light; they would lamb in February in their new environment and, under the influence of the decreasing daily amounts of light at that time, should certainly be in oestrus again by May. Since, for nutritional reasons, it is probably best to avoid pregnancy during lactation, the ewes could be mated in June. In subsequent years the mating season would conform to the usual time (autumn) in southern latitudes.

In recent years, flocks of Romney Marsh sheep have been sent from southern Australia to the tropical highlands of Papua and New Guinea. The elevation of this region is sufficiently high to provide temperatures suitable for raising British breeds of sheep, but the absence of any appreciable seasonal variation in the length of day raises interesting issues of adaptation. Sexual activity in this breed is normally regulated by seasonal light change and, in the absence of suitable light conditions, it may be expected that the animals will fail to exhibit their normal periodicity of reproductive activity. Many lambs from these Romney ewes have been born in the new environment (GRANGER, 1952) but it remains to be seen whether or not fertility problems will develop as, for instance, through haphazard, too weak, or even, possibly, complete failure of oestrus. However, judging by the behaviour of ferrets sent from England to tropical Africa (Duke of Bedford and Marshall, 1942), some of the ewes will probably exhibit oestrus throughout the year; from such ewes a strain of sheep may ultimately develop having no restriction in their time of breeding.

Merino ewes, in tropical regions of Australia, may be mated in either spring or autumn and, although the incidence of oestrus is possibly higher in autumn, a spring mating is preferred to ensure that ewes will lamb just after the highly seasonal rains in February or March. For these matings it is common practice to introduce Merino rams, purchased each year at the winter and spring stud sheep sales in temperate regions of southern Australia. Such introduced rams are frequently disinclined for work in October and November. MOULE (1950) points out that rams introduced into the tropics from temperate regions during mid-winter are subjected to an immediate increase in their daily level of lighting of from 40 to 60 minutes, at a time when the days are commencing to lengthen, and that this combination could well account for their poor libido. To offset the difficulty, Moule (1950) treated one group of four introduced rams to progressively reduced lighting in a small, darkened room each evening for six weeks prior to mating. After treatment their libido was excellent and, during three weeks commencing 24th October, they served all of the 372 ewes with which they were run. Untreated control rams remained uninterested in the ewes. This experiment supports the finding (Yeates, 1949) that seasonal fluctuations in fertility of the ram may be associated with light changes: it also illustrates one simple and practical way in which artificial control of the light environment may be used to overcome an important source of loss in animal breeding.

WINTER MILK FROM GOATS

With the knowledge that the breeding season of goats may be regulated by suitable modification of the light environment (Bissonnette, 1941; *U.S. Dept. Agric. Rpt.*, 1950), the possibility presents itself of arranging an autumn as well as a spring, kidding season for goats, so ensuring an even milk supply throughout the year. Goats' milk represents an appreciable proportion of the total milk available in many areas: the milk is used largely by persons to whom cows' milk may be unavailable and, owing to freedom from tuberculosis, it is in special demand for children's hospitals. For these reasons it might be considered worthwhile to arrange for half the herd to freshen in the autumn and thus make a strong contribution to the otherwise negligible winter supply of milk from goats.

There are other instances of the way in which knowledge of the effect of light and darkness on animals might be applied practically, and the foregoing should be regarded as examples rather than a complete list. Even these examples, however, should suffice to indicate that the light environment is a factor of considerable importance to farm livestock. With increasing recognition of this fact more intensive research is likely to be initiated and, in a field of enquiry so little explored, there are bound to be significant developments.

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